

THE EFFECT OF AGE AT WHICH ENRICHMENT IS COMMENCED
ON THE TEST PERFORMANCE OF THE WHITE RAT.

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ABSTRACT

Clarke (1968) hypothesised that the duration of the effect of early experience on behaviour would depend partly upon the potency and length of the experience, and partly on age at application of this experience, but particularly on the amount and duration of subsequent reinforcement of the experience. He argued that later enrichment could reduce the effects of early sensory deprivation on the behaviour of the animal. This thesis investigates whether animals show equal effects of enrichment after longer periods of deprivation, or whether the effects of deprivation are irreversible. The thesis also investigates whether a critical period for enrichment is in operation in the juvenile phase of a rat's life. Results indicate that no critical period is in operation, and that animals show equal effects of enrichment irrespective of the age at which they are enriched, and irrespective of longer periods of deprivation.

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1 INTRODUCTION

1.1 Origins of research into early experience

In the early 1930s Hall (1934) had been experimenting with the concept of emotionality in animals and the means whereby it could be measured. At about the same time Hebb was experimenting with the measurement of animal intelligence. These seemingly unrelated experiments were to combine into a research area that has relevance today.

The catalyst was provided in 1937 when Hebb blinded two groups of animals, one group as soon as their eyes opened, the other group at maturity. The two groups were compared by means of a variable pattern T-maze. Hebb found that the late-blinded group was consistently superior in performance to the group blinded at birth. This was one of the earliest indications that differential early environments influenced different abilities. The war interrupted research and in 1949 interest in enriched environments revived. In his Organization of Behaviour (1949) Hebb mentioned an exploratory study in which two groups of animals were reared under different conditions. One group was reared in laboratory cages in the normal manner, the other group was

reared as pets in a private home. At maturity the animals were tested on a variable pattern T-maze to determine the differences, if any, attributable to the differential environment. It was found that the home-reared animals were superior to the laboratory-reared animals.

The realization that environment influenced the capabilities of adult organisms provided a research topic for the next twenty years. Both Hall's work on the measurement of emotionality and Hebb's method of measuring animal intelligence became important in determining the effects of environmental differences. Both measures were developed and refined during subsequent years. Hall's work was expanded to include urination, ambulation, latency, rearing, and grooming, as well as defecation (Eriksen, Porter & Stone, 1948; Evans & Hunt, 1942). Hebb's closed field test was developed for water escape motivation and the procedure was considerably shortened (Rosvold & Mirsky, 1954). The environmental differences studied by Hebb were expanded to include noxious stimuli, administered to the animals at various ages.

1.2 Theoretical development

As a result of Scott's (1962) influence, the critical period hypothesis was adopted as an explanation of the differential environmental effect. Scott had been working primarily with

dogs and goats and had successfully isolated critical periods for the formation of social bonds in these animals. He reasoned that a similar process was in operation which accounted for the apparent differences between the animals raised in different environments.

Working alongside Scott in the investigation of these phenomena was Denenberg. He investigated the critical-period hypothesis thoroughly and concluded that the data fitted a stimulus-intensity hypothesis (Denenberg, 1964).

The accent of the research shifted in the mid 1960's and researchers were no longer as concerned with the way in which the environmental effect operated as they had been. The accent was now on the isolation of one variable amongst the many that appeared to give rise to the phenomenon. Researchers were now looking at what caused the phenomenon rather than how it occurred.

As a result, several hypotheses were advanced as possible answers to the question of which single variable caused enrichment. It was argued that temperature change was the significant variable in the experiments (Schaeffer, Weingarten & Towne, 1962). Another hypothesis was that movement of the animal was sufficient to provide the necessary stimulation. Experiments were done in which the cage was shaken for the stimulation period. Both temperature

and movement were found to be sufficient to provide the necessary effect (Levine, 1959).

During the 1960's research was undertaken into the physiological changes that occurred as a result of stimulation. The possibility that an enriched environment produced permanent physiological changes was first postulated by Hebb, and was developed by Kretch and his co-workers (1960, 1962). It was found that permanent physiological changes take place in an animal subjected to an enriched environment.

1.3 The problems of enrichment research

There was still, however, no coherent theory or factor that could adequately explain the phenomenon of early enrichment. This may have been because of the many variables that were manipulated by researchers in their experiments. King (1958) argued that this may have been the difficulty in formulating the explanation of the enrichment effects. For example, one of the variables manipulated by experimenters is the type of stimulation administered to the animal. Type of stimulation can be divided into two categories, mild and noxious. Mild stimulation is the term applied to animals placed in an enriched environment, or handled, while the term noxious stimulation encompasses electric shock, intense auditory stimulation or repeatedly throwing the animal into the air

and catching it. Rat pups are immature at birth: their eyes do not open until they are about two weeks old, and they seldom leave the nest before weaning. Because the animal is not in a position to take advantage of the environmental stimuli until after weaning, when the eyes are open and the animal can locomote freely, intense or noxious stimuli tend to be administered when the rat is juvenile. Stimuli presented to the animal prior to weaning must, therefore, be active stimuli. Although there was no adequate explanation, several factors emerged from the research. First, whether the stimuli were noxious or not, the effects were similar and the animals performed better on both emotionality and intelligence scales. Secondly, whether the stimulation was presented to the animal in infancy, the juvenile period, or in adulthood, the phenomenon was still noted.

Researchers appear to have ignored a basic aspect of research into enriched environments: that the enriched environment may not in reality be an enriched environment at all, but approximates the normal environment of the rat in the wild. Because researchers return the rat to a "normal environment" by means of stimulation, and then test it against a deprived rat, the studies are not of enrichment, but of deprivation.

1.4 The application to human development

Although researchers have neither learned the manner in which

early enrichment operates, nor which specific factor, if any, causes the enrichment, they have learned that manipulation of the environment increases the animals ability. Furthermore, Whimbey and Denenberg (1966) claim they have learned how to manipulate the environment in order to obtain required effects. The application of this concept provides a transition from animal behaviour to human behaviour. The concept of an enriched environment was applied to humans in the U.S.A. with a programme called Headstart (Gray & Klaus, 1965). The principle was the same: children from a poor environment were tested, provided with a period of enrichment, and retested. The enrichment period consisted of outings, games, painting, and drawing and similar pastimes. The retest scores of the children in the experimental groups were significantly higher than the retest scores of the children in the control groups, and were significantly higher than than the pre-enrichment test scores. These scores indicate that the phenomenon discovered by Hebb in the 1930's applied to humans as well (Clarke, 1968).

Because the results of the Headstart programme were promising, it was decided that a similar programme would be attempted at the University of Cape Town. This programme, aimed at alleviating the deprived environments of the Coloured children of the Cape flats, was called Grassroots. As was expected, the retest scores of the children in the Grassroots programme were significantly higher than the

pre-enrichment scores (Child, 1974).

There is some question, however, as to what constitutes an enriched or deprived environment. Although the requirements of an enriched environment will be discussed in chapter 4, the requirements of a deprived environment are also worth consideration. Examination of the literature shows that researchers do not generally report the deprived environment in as much detail as the enriched environment. Furthermore, the deprived environment is accepted as being deprived by default, and researchers do not query the degree of deprivation of any environment. It may be argued that the environment which is considered to be deprived is, in fact, a very rich environment by comparison to the environment of the animal in the wild. It has already been pointed out that the opposite may be true and it is suggested that the term "standard environment" should be used to avoid the connotations of the word deprived, and the possible confusion that may arise as a result of its usage. Nevertheless, in conformity with the literature deprived will be used throughout this thesis.

In the wake of this study, it was decided to return to the laboratory to investigate animals on as nearly a parallel condition as possible. It was also decided to investigate Clarke's hypothesis that

early learning will have effects which, if

unreinforced, will fade with time. It will not per se have any long term influence upon adult behaviour, other than as an essential link in the developmental chain (Clarke, 1968, p.1061).

Clarke thought that longer periods of deprivation did not cause a decrease in the animal's ability to recover from deprivation and that age was not a parameter of the enrichment process. He argued that the effects of deprivation are reversible and therefore the effects of enrichment are also reversible. It was decided to study the effects of different periods of deprivation and to attempt to determine whether increasing deprivation had an effect on the animal's ability to recover after enrichment. The result is the following experiment.

2 THEORETICAL DEVELOPMENT

2.1 The critical period hypothesis

2.1.1 The biological basis

During the early 1950s it was well known that environmental enrichment had a considerable effect on the behaviour of an animal. The way in which this effect occurred, and why, was, however, unknown. It had long been known in the biological sciences that interference in the developmental processes of an embryo could produce bizarre results. In 1921 Stockard had noticed that the treatment of an embryo with chemicals caused deformations. Originally he thought that the deformations were the result of the specific chemical used, but further experimentation showed that effects were the same, irrespective of the chemical used, as long as the time of application was constant (cited in Scott, 1962). In this way it was shown that critical periods for biological development existed in the embryo. When this critical period was interfered with the resulting deformation was always the same, and was dependent upon which part of the organism was developing most rapidly at the time.

2.1.2 The psychological impetus

At the same time Freud introduced his theory of neurosis. He theorised that fixation was one of the bases of neurotic maladjustment. In Introductory Lectures on Psycho-Analysis (1922) he wrote:

it [fixation] is a universal trait common to every neurosis, and one of great practical significance....In the majority of cases it is actually a very early phase of the life history which has been thus selected, a period in childhood even, absurd as it may sound, the period of existence as a suckling infant....The traumatic neuroses demonstrate very clearly that a fixation to the moment of the traumatic occurrence lies at their root. (p.232)

Freud contributed to the idea that early experience affected adult behaviour, and some of the early research was conducted to determine whether early traumatic experiences fixated animal behaviour (Fuller & Waller, 1962). Application of noxious stimulation to animals in infancy investigated whether the animals showed traumatic fixation. Contrary to Freudian expectation, experiments indicated that stimulated animals were better problem solvers with less emotional activity than non-stimulated organisms (Griffiths & Stringer, 1952).

2.1.3 The contribution of comparative psychology

In 1935 more evidence was added to the critical period concept. Konrad Lorenz, extending Heinroth's findings,

noticed that birds reared by hand developed filial and social responses to their keeper rather than to their species (Hess, 1962). He called this process imprinting as the impression of the mother-object on the young animal was rapid and appeared to be stamped in. Imprinting refers to a primary social bond formation in young animals and Lorenz postulates that an animal's early social experiences are important in determining social and sexual behaviour in adulthood. There appeared to be a critical period in the early life of the animal during which experience of the mother had to occur in order to result in any attachment. Lorenz hypothesised that the imprint governed not only social but also sexual behaviour; imprinting was therefore related to both social responses and evolution.

In the development of the critical-period hypothesis, three distinct critical periods were isolated (Scott, 1962). There is a period for the formation of social relationships, for learning, and for infantile stimulation. A critical period is the existence, in the developing organism, of a period optimal for the formation or development of bases of adult behaviour. The mechanism of critical periods is unknown, but it is believed that a stage is reached in the developing organism which permits the learning of specific behaviours. After a time, irrespective of whether the behaviours have been learned or not, the stage passes; and the subsequent learning of those behaviours, if unlearned, may be

permanently impaired. For example, until a certain stage in development has been reached it is impossible to teach a human child the concept of conservation of volume. A stage in the development of the child is reached, however, when conservation of volume becomes understandable and can be easily taught (Beard, 1969). Although children can apparently learn conservation of volume at any time after the occurrence of the critical period, there is considerable evidence that the behaviour of animals is permanently impaired by overt interference in the critical period (Harlow, 1962; Hess, 1962; Scott, 1962). The formation of social and sexual bonds was thought to take place in animals in the same way.

As a result of these factors, the critical-period hypothesis gained popularity as a possible means of explaining the effect of environmental enrichment. Scott had shown the existence of definite critical periods in the behavioural development of dogs and goats. He had shown that socialization in dogs and in goats was dependent upon interaction with their peers, and the interaction had to occur at certain times in order to be effective. Harlow and Harlow (1962) had reported similar findings in relation to sexual and maternal behaviour of rhesus monkeys. Furthermore, Scott (1962) had determined when the critical periods occurred in the developing dogs, and it seemed possible to relate these effects to rats.

2.2 The search for the critical period

Because a critical period in behavioural development can occur at any time after birth, it was necessary for researchers to develop a system of stimuli which could be applied to infant rodents as well as adults. It was equally important to develop a series of tests which would measure changes in the behaviour of animals as a result of stimulation. These behavioural measures will be discussed later.

The need for a system of stimuli led to the development of mild and intense systems of stimuli which were used on infant and adult rodents. This gave rise to disparate findings concerning the effect of noxious stimuli on infants. Some researchers found that intense stimulation delivered at an early age was negatively correlated with the animal's learning ability (Eriksen, Porter & Stone, 1948) while others found that intense stimulation at an early age had no noticeable effect, but that as the animal grew older, so the reaction to stimulation increased (Griffiths & Stringer, 1952). Other authors found that animals were positively affected by intense stimulation at an early age (Levin, 1962; Spence & Maher, 1962) and by short periods of intense stimulation in the first ten days of life (Denenberg, 1962; Denenberg & Kline, 1964).

Experiments that require the animal to be aware of its environment are usually conducted from the time of weaning onwards, and tend to show greater similarity of results. It has been shown that animals which have spent time in the enriched environment show behavioural differences from animals that are not treated (Beach & Jaynes, 1954; Denenberg & Morton, 1962; Forgays & Forgays, 1952; Whimbey & Denenberg, 1966). Hymovitch (1952) found indications that the enriching experience must occur before adulthood in order to have the required effect. Forgus (1954), on the other hand, found that the experience must occur very early in the life of the animal to be effective. It was also found that animals exposed to the enriched environment immediately after weaning were significantly better problem solvers than those exposed at a later age (Forgays & Read, 1962).

It was not known what specific factor of the environment caused enrichment. Several experiments were conducted to determine whether purely visual experience was sufficient to cause enrichment, or whether locomotion in the enriched environment was a parameter of the enrichment experience. It was found that animals allowed to locomote freely in the environment were more enriched than restricted animals in the same environment (Forgays & Forgays, 1952; Woods, 1959). It was also determined that animals restricted in locomotion but with a view of the environment were better problem solvers than animals reared in the normal laboratory manner (Forgays

& Forgays, 1952). Hymovitch (1952) found that the the effects of rearing in the enriched environment were stable and apparently permanent, and that the animals reared in an environment with playthings were superior to animals reared with only running wheels in the cages. Although there was some doubt as to the exact time at which enrichment should take place and as to the actual factor that caused the process, there was no doubt that enrichment caused behavioural effects.

Research was continued on these fronts: the critical period for enrichment as well as a single causative factor was sought. These are dealt with separately.

2.2.1 Problems in isolating critical periods

King (1958) observed that the isolation of a critical period for development was hampered by:

Seven recognisable variables ... of particular significance to the experiments....They are: (a) the age of the animal when experience is given, (b) age at the time of the test, (c) the duration or quantity of the experience, (d) the type or quality of the experience, (e) the type of the performance task required of the adult animal, (f) the method for testing persistence of effects, and (g) the relation of the experience to the genetic background of the animal. (p.46)

These seven variables will be dealt with in turn.

2.2.1.1 Time of enrichment

In the infantile period of life investigators have either provided an enrichment for the duration of infancy (Griffiths & Stringer, 1952; Levine, 1959), or have subdivided the period into long sections (Denenberg, 1962; Denneberg & Smith, 1963) or have given short periods of intense stimulation (Denenberg & Kline, 1964). In the juvenile phase experience is usually begun shortly after weaning, and is continued until sexual maturity (Hymovitch, 1952) or beyond into adulthood (Forgays & Read, 1962; Woods et al., 1960). On the other hand, many investigators begin the process in adulthood and continue until death (Forqus, 1956). Thus the age at which the experience can be given varies through a considerable period.

It has already been mentioned that some researchers found early experience was more beneficial to the animal than late experience. Forqus (1956), for example, found some evidence that visual enrichment in infancy was more important than visual enrichment later in the animal's life. This contradicts findings by Hymovitch (1952). Other experiments indicate that the effects of enrichment are permanent (Denenberg et al., 1968), that early experience is more effective than late experience (Denenberg & Morton, 1962) and that irrespective of the age of animal when experience is given, enriched animals are superior to non-enriched animals

(Greenough, Madden & Fleischmann, 1972). It has been impossible to isolate a critical period on the basis of age alone. In comparison with the age periods immediately before and after treatment there appears to be no period during the development of the animals when administration of enrichment causes a large and lasting difference to adult behaviour.

2.2.1.2 Time of testing

As with the enrichment process, the time of testing can vary considerably, and is usually determined by the effects that the researcher wishes to investigate. For example, some experimenters wanted to examine immediate effects of enrichment and tested as soon as the treatment was concluded (Ader & Belfer, 1962). Others wished to examine later effects and allowed a period of time to elapse between treatment and testing. The period between treatment and testing was not constant, and ranged between 10 days (Bingham & Griffiths, 1952), and 150 days (Denenberg & Morton, 1962a). Some authors used a convenient three month period (Bernstein, 1952; Denenberg, 1962). One group of experimenters was interested in the long-term effects of the training, and allowed long periods to elapse between treatment and examination. This category includes those experimenters who conducted longitudinal studies (Denenberg & Smith, 1963; Denenberg et al., 1968; Woods et al., 1960). Yet others were interested in maturation effects and tested while the animals were still

undergoing enrichment, and the testing can even be considered a part of the enrichment process (Woods, 1959).

2.2.1.3 Duration of experience

The third variable mentioned by King (1955) is the duration or quantity of the experience given to the animal. As with the previous examples, there have been large variations. Some researchers gave the subjects as little as three minutes of stimulation per day (Denenberg & Smith, 1963), while others gave prolonged periods of stimulation (Forgus, 1955). Obviously, experimenters were not restricted to the use of only one period of enrichment, and some used different durations for their treatments. Woods (1959) for example, used two enrichment periods of different lengths at different ages of the animal.

Intense stimulation can only be administered for short periods, because long periods may kill the animal. When the stimulation is mild, however, the animals can be left in the enrichment situation for longer periods of time. Shorter periods spent in the enrichment situation were generally during the course of experiments using noxious stimulation of the subjects.

It therefore becomes important to discuss not only the exposure length but also the number of exposures in the

duration variable. While Denenberg and Smith (1963) exposed their test animals for three minutes there were ten exposures, making a total of thirty minutes of noxious stimulation. The duration variable is complicated by the fact that non-noxious stimuli were administered for very much longer periods of time (Denenberg & Morton, 1962a). In the majority of the enrichment experiments using mild stimulation the animal was placed in the enriched environment and allowed to live in that environment for a length of time.

It was noticed that animals treated with noxious stimuli required shorter periods for the stimulation to have a permanent effect (Denenberg & Kline, 1964). This appears to present an anomaly relating to this type of stimulus, for imprinting of a young duckling is a rapid process, and cannot be regarded as a noxious stimulation (Hess, 1962).

2.2.1.4 Type of experience

Experiments with varying types of experience are as different as highly inventive minds can make them. Generally, these experiments may be grouped in terms of three types of experience: those involving stress, those involving handling, and those involving environmental manipulation.

Within the stress category, electric shock features prominently, sometimes constant (Denenberg & Kline, 1964),

and sometimes with varied shock levels (Denenberg & Karas, 1960). Often shock is mixed with other treatments such as handling (Denenberg & Bell, 1960) or food deprivation (Broadhurst, 1957). Other methods of inducing stress in animals include temperature change (Schaeffer et al., 1962), shaking (Levine, 1959) and audiogenic seizure (Griffiths & Stringer, 1952).

In the handling category different types of handling were devised. These included removal of animal to another cage for a short period (Denenberg et al., 1962), continuous and interrupted handling (Bernstein, 1959) and, overlapping with previous variables, handling at different ages (Denenberg, 1962; Whimbey & Denenberg, 1967).

Finally, environmental manipulation allowed comparisons between animals reared in an enriched environment and in laboratory cages (Denenberg et al., 1968), in an enriched environment and squeeze boxes (Bingham & Griffiths, 1952), and in mesh cages restricting locomotion but permitting a view of the enriched environment (Forgays & Forgays, 1952). Others provided animals with a visually enriched environment (Forgus, 1955; Forgus, 1956).

2.2.1.5 Task required of the animal

The fifth variable of interest in determining critical

periods is the type of performance task required of the animal. This variable can be divided into two main categories: those tasks investigating the emotionality of the animal, and those investigating the problem-solving ability of the animal. Within both of these categories there are considerable variability. The original test for emotionality was conducted in an arena 2,44 meters in diameter, painted white and divided into segments by black radial and concentric lines (Hall, 1934). Broadhurst (1957) determined that the arena size was not crucial to the outcome, but that a smaller arena gave increased measures of emotionality. As a result, many different types of arena were used, varying from 0,81 meters square (Denenberg & Smith, 1963) to a 1,52 meter square arena (Ader & Belfer, 1962). Some arenas were rectangular (Werboff & Havlena, 1962).

Although the arena size is unimportant from the point of within-experiment effects, arena size has an effect on the measures used. This makes between-experiment comparison difficult, a difficulty compounded by the different types of measures used and the uncertainty regarding their reliability and validity. The different measures ranged from the quantity defecated (Hall, 1934), to the consumption of food (Whimbey & Denenberg, 1966) and water (Spence & Maher, 1962). Other measures included urination (both frequency and volume), ambulation, grooming, latency, squealing, and

inner-circle activity. Most authors used defecation and urination as routine and a selection of the other possible measures.

In the investigations of the problem-solving ability of the animal there is no less variation. Different types of mazes were used, comprising the variable T-maze (Forgus, 1954, 1955, 1956), the T-maze (Forgus & Read, 1962), the inclined-plane maze and Lashley jumping test (Bingham & Griffiths, 1952). Other experimenters used a simple avoidance learning technique (Denenberg & Karas, 1960, Denenberg & Klein, 1964), while still others used an underwater Y-maze (Karas & Denenberg, 1961). Some experimenters used the Hebb-Williams maze and the variations attached thereto.

The systems of measurement used in these tests were not standardized and although they generally fall into two groups, being time to reach the goal and number of errors made by the animal on the way, the time to run a T-maze cannot be compared with the time to run the Hebb-Williams. Furthermore, the time to run the sub-tests of the Hebb-Williams varies considerably. Once again, therefore, within-experiment measures of animal performance are comparable, but between-experiment comparisons are impossible.

In the fifth variable, two factors have been isolated. They

are the mechanics of the performance task devised by the researcher, and the method of scoring the performance of the animal as it moves within these mechanics. It is partially as a result of this variability that it was decided to use the Hebb-Williams test and Hall's open field test to determine the differences due to environmental enrichment. In both these procedures the equipment is well documented and the scoring systems used are well reported. In an effort to maintain a standard experiment it was determined to use the systems previously reported. As will be seen, practical considerations in the application of the experimental technique forced the change of some of the standards.

2.2.1.6 Method of testing for persistence

The sixth variable is the method of testing for persistence of effects. One of the tenets of early enrichment is that the effects are permanent (Beach & Jaynes, 1954). Different methods have been used to measure persistence. One method has been to treat animals and test immediately after treatment, thereupon to return the animals to the normal laboratory environment, and to test the same animals at a later date (Ader & Belfer, 1962; Furchtgott et al., 1961). Another method is to treat the animals in youth, but only to test the animals in adulthood (Denenberg et al., 1962; Karas & Denenberg, 1961).

The advantage of the latter method is that the adult test cannot be contaminated by the earlier test given immediately after treatment. Both methods suffer from the disadvantage that the animals are returned to the laboratory environment for an extended period of time prior to testing for persistence. Another method is to leave the animal in a test situation for an extended period of time and to make a continuous series of observations throughout the period (Levine, 1962). This procedure cannot, however, be used with the open field or Hebb-Williams tests. These tests rely on the animal being familiar with the test area and being unfamiliar with the specific problem.

A third method of testing for persistence was employed by Denenberg and Smith (1963) who tested independent groups at various ages. The procedure:

would be to give the same treatment to several groups of animals at the same age and test them at different adult ages. Such an experiment should be designed to isolate and evaluate interactive effects. (King, 1958, p.53)

Most of the methods of testing for persistence of effects run the risk of having the variables contaminated by other experience. The effects of early experience may be destroyed or enhanced by later experiences that the animal undergoes. It is impossible for the animals to be kept in vacuo, and it cannot be argued that the effects will be similar for both groups because the treatment causes behavioural changes in the animals of the experimental group.

2.2.1.7 Genetic background

The last of King's seven variables is the relation of the experience to the genetic background of the animal. Fortunately, genetic effects are relatively easy to control for in the laboratory experiment. This is accomplished by mixing the groups of animals after birth in a random fashion, so that any of the experimental groups contain a cross-section of litter members. Nevertheless it is important to realise that this variable has a significant effect on the outcome of an experiment (Broadhurst, 1957; Whimbey & Denenberg, 1966).

This examination of King's seven variables has demonstrated not only the variability possible in this type of experiment, but also, because of this proliferation of measurement systems, the difficulty of arriving at a theoretical position which adequately explains all the aspects of the phenomena reported in the literature. These were the problems with which the hypothesis had to contend. In many instances the results of experiments appeared to be conflicting, and in others the variables differed so much as to make any appreciation of the ramifications of enriched environments impossible.

2.2.2 Difficulties for the critical-period hypothesis

One of the arguments against the critical period hypothesis is that enrichment has an effect on the animal, irrespective of when treatment takes place. A requirement of the critical period hypothesis is that enrichment takes place at a specific time in the development of the animal in order to produce a pronounced effect. It should be noted that it is not contended that an enriching experience will not give rise to increased performance, but that enrichment at a specific age will cause an increase in performance over what may normally be expected.

The critical-period hypothesis requires that the duration of the stimulation be limited to the parameters of the critical period. In other words, if the critical period for development by enrichment is ten days long, then stimulation for less than ten days should not cause as great a difference between experimental and control groups as stimulation for the full ten-day period. Similarly, stimulation for more than the ten-day critical period should produce decreased increments in the between group differences.

These aspects of the critical-period hypothesis were fundamental. Apart from the problem of more or less even gains at all ages of enrichment, it can be seen that more intense or noxious stimuli need to be administered for

shorter periods. This is also contrary to the critical-period hypothesis. Denenberg (1962) noted that both number of days handling, and age at which handling occurred were critical parameters affecting the later behaviour of the animal. This seems to support the critical-period hypothesis, indicating that the earlier the enrichment, the more beneficial the effect, but the exact time at which the handling should occur in order to maximise the effect could not be isolated. This, and the dependence of the effect upon length of stimulation, both mitigate against the critical-period hypothesis.

Furthermore, the quality of the experience, obviously a parameter of the effect, cannot be accommodated by the critical-period hypothesis, which requires that benign or noxious experience in the critical period will result in approximately equal effect. Yet it is apparent that intense stimuli need be applied to the animal for a comparatively short period before a significant difference is noted between the stimulated and non-stimulated groups. For these reasons the critical-period hypothesis fell into disfavour and Denenberg (1968) developed the stimulus intensity hypothesis in an attempt to explain the phenomenon of enrichment.

2.3 The stimulus intensity hypothesis

The stimulus-intensity hypothesis was originally considered

by Hebb (1949), although it was not presented as a hypothesis. Hebb argued that the organization of adult behaviour is largely determined by the quality of infant experience and learning. This early learning is important because it produces permanent changes in the structure of the central nervous system. In this way he laid the foundations for both the stimulus-intensity hypothesis and also for the physiological research that followed in later years.

Denenberg's early work was directed towards the development of the critical-period hypothesis: he was a believer in the effects of critical periods on the development of mammals (Denenberg, 1962; Denenberg & Bell, 1960; Denenberg & Karas, 1960). As his research progressed, however, he found that the critical-period hypothesis was an inadequate explanation for enrichment effects, and he began to investigate theoretical considerations of his own. He realised that enrichment was a complex interaction of King's seven variables, and was particularly interested in the effects of age and length of experience (Denenberg, 1962a; Denenberg & Smith, 1963). From this he developed a theory that infantile stimulation caused stress for the animal, which increased the animal's tolerance to stress in later life. Denenberg found evidence to support this theory (Denenberg et al., 1962b) and his stimulus-intensity hypothesis was the result. Further support of the hypothesis confirmed the concept of exposure to stress accustoming the animals to stressful conditions,

thereby ensuring that when the animals encounter a stressful condition in later life they can cope better by virtue of experience (Denenberg & Smith, 1963; Karas & Denenberg, 1963; Lindholm, 1962).

2.3.1 Stimulus intensity vs. critical period

Because of accumulating research evidence in support of a stimulus-intensity hypothesis, Denenberg & Kline (1964) suggested that stimulation of rats in the first ten days of life by handling caused significantly faster learning of an avoidance task (Denenberg & Karas, 1960). Denenberg (1962) tried to ascertain whether shorter periods within the first ten days would yield similar results, and found that animals handled between days six and ten were superior to other groups, and that there were no significant differences between the other groups. They thought that either of two hypotheses could plausibly explain these differences: the critical-period hypothesis and the stimulus-intensity hypothesis. A basic concept underlying the critical-period hypothesis is that there is a limited period during which a particular stimulus will have profound effects, and the Denenberg (1962) data seemed to support this hypothesis.

The other possible explanation for this effect is stimulus intensity. Denenberg and Kline (1964) contend that the infantile rat is immature, and therefore a mild stimulus may

not trigger the mechanism whereby the animal is enriched. A stronger stimulus, however, would trigger such mechanisms and cause the animal to become enriched at a earlier age. This argument is congruent with the fact that animals treated with a mild stimulus respond better at a later age (Denenberg & Morton, 1962b).

The purpose of the experiments reported here was to compare these two hypotheses by stimulating rat pups at different times within the first five days of life with electric shock. It is assumed a priori that the intensity of stimulation from electric shock is greater than that from handling. If the intensity hypothesis is correct, then increasing the amount of stimulation the rat receives during the first five days of life should result in a significant improvement in avoidance learning. However, if the critical period hypothesis is the more accurate model, then the prediction is that the stimulated group should not differ from the non-stimulated controls since stimulation occurred prior to the onset of the critical period (Denenberg & Kline, 1964, p.2).

Results showed that the younger groups responded better to electric shock than they had to handling, and:

In order to account for these as well as other findings (Denenberg, 1962) within the context of the critical period hypothesis, it seems necessary to posit different critical periods for different forms of infantile stimulation (for example, shock, handling) as well as different adult dependent variables. The intensity hypothesis appears to be more parsimonious (Denenberg & Kline, 1964, p.5).

Denenberg's stimulus-intensity hypothesis was developed to the extent where it was regarded that emotional reactivity is reduced as a monotonic function of the amount of stimulus input in infancy. Denenberg (1964) postulated an inverted "U" function to assist the theoretical assumptions, and incorporated the Yerkes-Dodson law into the hypothesis. This

law states that the optimal level of motivation for a task decreases as task difficulty increases (Broadhurst, 1957).

2.4 Problems for the stimulus intensity hypothesis

Spence and Maher (1962) examined the effects of two types of treatment, handling and intense auditory stimulation, on emotionality. The treatments were administered at an early and late age. Emotionality was inferred inversely from water consumption in both a novel situation and the same situation after administration of an electric shock. They failed to find evidence of a monotonic relationship.

Apart from not being able to accommodate certain data, Denenberg's stimulus-intensity hypothesis was also inadequate in another respect. In terms of the stimulus-intensity hypothesis, a monotonic relationship exists between stimulus in infancy and emotional reactivity. Furthermore, because a young animal was immature it required a more intense stimulus than an old animal. Yet Denenberg cannot, and does not, hypothesise that the earlier stimulation is more enriching than later stimulus. It is assumed that all animals will, apart from individual differences, become equally enriched as a result of an enriching experience.

It is also assumed that the time of the enrichment is unimportant, and that older animals which are enriched or, in

Denenberg's terms, presented with stimuli, will also become enriched. The monotonicity hypothesis, if applied over age, follows the developmental model with respect to walking: children may start at different ages but, with the exception of the severely retarded, all children learn to walk. In this there are two problems for the hypothesis. Unless Denenberg postulates an age beyond which stimulus intensity is no longer operable, which he cannot do for it would make the stimulus-intensity hypothesis reliant upon a critical-period model, he must accept that if two groups of animals at the same age are presented with mild and intense stimuli, the intense stimuli should cause the animal to show greater behavioural differences than the mild. There is no evidence that intense stimulation is more effective than mild stimulation in adulthood.

The other problem with the stimulus-intensity hypothesis is its inability to explain differences between early and late stimulation, as it has been shown that the effects of early stimulation are both greater and longer lasting than the effects of late stimulation (Denenberg et al., 1968; Forqus, 1956).

Further data showed the inadequacies of the stimulus-intensity hypothesis. Denenberg and Haltmeyer (1967) found that animals handled for varying lengths of time in infancy showed a positive relationship between length of

handling time and amount of free circulating corticosterone in the animals' blood. Prior to decapitation, the animals were placed in an open field. Shock was administered to half the group. According to the stimulus-intensity hypothesis the shocked animals should have had higher levels of serum corticosterone than the unshocked animals. Results did not support this thesis.

Furthermore, the Yerkes-Dodson law was repealed in 1965. Brown (1965) argued that the evidence for the Yerkes-Dodson law was not adequate to prescribe a relationship where task difficulty and optimum motivation were inversely related. He showed that the acceptance of any law required a two-stage proof, which condition has clearly not been met.

From the research presented it is apparent that while neither the critical-period hypothesis nor the stimulus-intensity hypothesis were able to explain totally enrichment, both appear to have value in explaining aspects of the enrichment process. For example the critical-period hypothesis can be used to explain why handling after infancy does not have the same effect as handling in the first three weeks of life (Levine, 1956), and why problem-solving behaviour is improved more by free-environment experience during the second three weeks of life than during infancy (Denenberg, Woodcock & Rosenberg, 1968; Forgays & Read, 1962).

In general, it appears that stimulation in the first three weeks of life affects the emotional reactivity of the animal, while later stimulation affects the problem-solving ability of the animal. The critical-period hypothesis can be used to understand why infantile handling has no effect upon the performance of the animal in the Hebb-Williams test (Denenberg & Morton, 1962; Schaeffer, 1963), and why animals stimulated between the sixth and tenth day of life show less reactivity than others stimulated during earlier and later periods (Denenberg, 1962).

Yet, the critical-period hypothesis is unable to explain the effects that caused Denenberg to develop the stimulus-intensity hypothesis, and in the same way the stimulus-intensity hypothesis is unable to explain all the features of early stimulation. It is perhaps best to accept that both hypotheses have merit and that the most useful method of describing the enrichment process is in terms of both.

Nevertheless, the stimulus-intensity hypothesis was used to explain facets of enriched behaviour that the critical-period hypothesis had been unable to do. Apart from explaining the fact that early enrichment requires shorter periods to be effective than does late enrichment, the stimulus-intensity hypothesis also provides a reasonable explanation for the fact that stronger stimuli, presented at an early age, result

in a significant difference in behaviour, while weaker stimuli do not (Denenberg et al., 1962). As a result of these factors, and a change in the attitude of experimenters, the stimulus-intensity hypothesis had short lived popularity.

2.5 What caused enrichment process?

The change in attitude of researchers is reflected in the literature as a move away from the question of whether enrichment took place as a result of a critical period, or stimulus intensity. They began to be more concerned with what constituted an enriched environment.

They knew from early experiments that playthings introduced into the cage would cause enrichment, that handling, shock, auditory stimulation, and a host of other factors would cause the same effect. Researchers turned their attention to attempting to determine which factor, common to all these procedures, could have contributed to the enrichment process.

Some experimenters thought that handling was the single most important effect of the enrichment process, and experiments have shown that handling the animals was an enriching process, causing them to perform better on the open field and Hebb-Williams test (Radloff, 1959), that there were physiological effects (Rosenzweig, 1966), and that handled rats had greater viability on a termination schedule (Bovard,

1958).

2.5.1 Shaking the cages

The search for the underlying effect began at handling. Levine (1959) put forward the hypothesis that a component of handling and all the other enrichment procedures was movement of the animals. He wrote:

Although the nature of infantile experience has been seemingly diverse, there is one common element present in all the treatments, namely that it has been necessary to handle the animal in order to initiate the experimental treatments. (Levine, 1959, p.243)

It had been shown that handling of the animals was not the important feature of the enrichment process, but that if the animals' cages were moved, without human contact with the animal, then the animal was enriched. There were no significant differences between animals handled by humans and the animals whose cages were shaken (Levine, 1959; Levine & Lewis, 1959).

It was noted by Levine and Lewis (1959) that handling seemed to have a significant effect on adrenal ascorbic acid depletion. Animals were subjected to cold stress and it was found that adrenal ascorbic acid depletion was affected by handling. There were significant differences between all the experimental groups and the control group, but there were no differences between the experimental groups.

2.5.2 Temperature changes

Perhaps as a result of this study, the question of whether temperature change could be the fundamental variable causing the enrichment process was posed (Schaeffer, Weingarten & Towne, 1962). The argument was that in all the handling experiments the animals were removed from the nest and the warmth of the mother. It had been shown that removal of the mother from the litter resulted in no significant behavioural changes in the young (Levine & Lewis, 1959). Schaeffer et al. postulated that as the enrichment was not a result of separation it could possibly be a result of temperature change in the animal's surroundings. They hypothesised that the warmth of the experimenter's hand in the handling process increased the enrichment process.

Although it is possible that both movement and temperature change are factors of the enrichment process of the animal, recent experiments have indicated that handling is only a small part of the whole process of enrichment. It has been found that handling reduced straight alley running time in an animal, but the scores on Lashley III maze learning were unaffected. Both groups, those which had been handled and those which had not were found to be inferior to littermates reared in an enriched environment (Greenough, Madden & Fleischmann, 1972).

While these studies did not provide the common denominator of enrichment processes, they indicated the growing use of physiological techniques in the determination of the effects of enriched environment.

2.6 Physiological considerations

In 1949 Hebb had stated that he thought the effect of enriched environments was due to cortical changes which take place as a result of enrichment. This idea was developed by Bovard (1958) who showed that early handling effects on viability were mediated by a seemingly permanent change in the balance of hypothalamic activity in the anterior region. He indicated that this resulted in increased growth hormone, and decreased pituitary adrenal cortex and sympathetico-adrenal medulla systems under stress conditions. He also noted that the alteration in hypothalamic balance was a result of change in the amygdaloid complex activity arising, Bovard thought, from the sensory input of early handling.

Another aspect of brain activity that was measured was Cholinesterase (ChE) activity. It was found that enriched animals had significantly lowered "sensory cortical specific ChE activity" (Zolman & Morimoto, 1962, p.800). When these animals were replaced in a standard laboratory environment prior to ChE measurement, the ChE levels dropped to non-significant levels, indicating that the changes were not

permanent. Zolman and Morimoto also found that the age at which enrichment began was not important, nor did subcortical ChE levels drop during a thirty day laboratory cage isolation. Also, enriched animals were significantly higher in sensory and dorsal cortical weight, but there were no differences in subcortical or total brain weight.

Other studies appeared, which showed that training and environmental complexity had an effect on the brain of the animal, notably in brain chemistry (Kretch, Rosenzweig & Bennett, 1960). The cortical-subcortical ratio relationship to enrichment was again examined and was found to be significantly different (Kretch et al., 1962).

This research was extended to include other changes in brain chemistry (AChE), physiology (number of glial cells, scatter of neurons), and morphology (brain thickness and weight) (Rosenzweig, 1966; Rosenzweig, Bennett & Diamond, 1972). Results of these studies show that the enrichment process has a profound effect upon the physiology and chemistry of the animals' brain.

2.7 Overview

In reviewing the literature on environmental enrichment research performed on rats it is easy to reach the conclusion that there is no realistic theoretical viewpoint; that the

use of different variables by various experimenters has led to such a proliferation of different and sometimes spurious results that little in the way of a unified concept of the mechanism of enrichment can be abstracted. It is hardly exaggerating to say that a theory of enrichment, whether dependent upon critical-period concepts or stimulus-intensity concepts, whether based on movement or temperature changes, will be challenged by literature which will provide contradictory evidence.

It is perhaps for this reason that researchers had to content themselves, until the phenomenon was better understood, with the realization that, for whatever reason, enrichment worked.

Beyond this, however, was the knowledge that researchers could manipulate the environment of the animals, and produce desired effects (Whimbey & Denenberg, 1966).

From the seemingly endless contradictions and variability of enrichment experiments:

The evidence obtained thus far has raised the question of what in this area constitutes the major experimental treatment. It appears that the condition of no treatment seems to have the most profound effect upon development and the subsequent emotionality and performance of the animal. Thus far in all of the experiments coming out of our laboratory it has been the non-stimulated infant that has exhibited relatively slower development, greater emotionality and poorer performance in adulthood. (Levine, 1959, p.245-246)

It is also necessary to examine the means whereby the

animals' behaviour was measured in order to understand fully the implications of these developments. In the next chapter therefore, these measuring devices will be discussed.

3 MEASURES OF ANIMAL PERFORMANCE

3.1 Emotionality

Hall (1934) introduced the concept of emotionality in rats, and the means whereby this could be measured. He defined emotionality as:

the state of being emotional. This state consists of a group of organic, experiential and expressive reactions and denotes a general upset or excited condition of the animal....The reader is warned against interpreting emotionality as a thing or faculty. It is merely a convenient concept for describing a complex of factors. (Hall, 1934, p.385)

He proposed that urination and defecation be used as measures of emotionality, because there were known instances in which high level fear had produced involuntary evacuation, notably on the battle-field. He realised that to validate defecation and urination as measures of emotionality he would have to correlate them with other measures of emotionality. He reasoned that a high condition of emotionality would prevent the animal from satisfying needs. An animal was deprived of food prior to being placed in an open field, a large circular arena with which the rat was unfamiliar. Hall felt that the unfamiliar surroundings would cause a state of high emotionality in the animal, which would prevent the animal from satisfying hunger. He wrote that:

when rats are placed in a strange enclosure the number of rats defecating and urinating decreases from trial to trial until practically all defecation and urination has ceased. Moreover, if food is present in the field and the rats have not been fed for some hours, the decrease in number of animals defecating and urinating is accompanied by a rise in the number of animals eating food. This correlation substantiates the hypothesis that defecation and urination under these conditions is truly emotional. (Hall, 1934, p.387)

3.1.1 Ambulation and emotionality

Hall (1936a) developed and extended these findings with the knowledge that hungry rats are less emotional than satiated rats, particularly when there is food in the open field. He hypothesized that the need for food was sufficient to enable the rat to overcome initial fear in the open field.

Hall (1936b) also attempted to relate emotionality to ambulatory activity. He examined the relationship between defecation, as a measure of emotionality, and the ambulatory speed of the animal. He found that slower moving animals defecated more than faster animals and, according to his paradigm, they were therefore more emotional. He countered the argument that slower rats are slower because they are defecating by pointing out that animals often defecate on the move. Comparing trials when the animal defecated to trials when the animal did not, Hall found that activity on defecating trials was not significantly different from non-defecating trials for the same animal.

Broadhurst (1957) confirmed Hall's results in a study in which he controlled for the factors which had been ignored up to this time. Experimenters had been using animals with different backgrounds and it had been suggested that the effects of strain differences, age, and sex differences as well as previous experience and husbandry were confounding the experimental variables (Christie, 1951). Broadhurst found that defecation scores characteristically declined with increasing exposure to the open field, but that ambulation scores did not decline after an initial drop. He found that male rats defecated significantly more than female rats, and that female rats were significantly more active than males. He thought that this indicated a real difference between male and female animals.

Further evidence against ambulation as an effective measure of emotionality indicated that ambulatory activity was directly linked to the age of the animal (Furchtgott, Wechkin & Dees, 1961). Exploratory behaviour was operationally defined and it was found that all the indices of exploration showed a significant inverse relationship with age. This was confirmed in a longitudinal study which showed a significant decrease in the activity levels of animals over time (Werboff & Havlena, 1962). Although age appears to be a significant factor affecting ambulation in the open field, Werboff and Havlena found that only large age differences affected ambulatory activity: when age differences were small, the

apparent effect is small.

Thus results of attempts to relate defecation and ambulation have not been consistent; both Denenberg and Morton (1962) and Hall (1936) reported significantly negative correlations.

These correlational studies have been instrumental in initiating the thesis that high defecation and low activity are related and measure the same behavioural component i.e. emotionality.

Studies opposed to this thesis fall into 3 groups. First, studies which report correlations not significantly different from zero (Anderson, 1938a and b). Second, studies which note that contrary to expectations, ambulation does not increase as a function of increased exposure to the open field (Broadhurst, 1957, 1958a and b; Candland, 1962). Since defecation decreases on successive testing days, an increase in ambulation would be expected as the animal adjusts to the mild stress of the open field. Third, strains judged as emotional (i.e. high defecators) are not necessarily the least active strains (Broadhurst, 1958b). (Pare, 1964, p.19)

Pare (1964) used measures of ambulation, defecation, rearing, latency, urination, and squealing, and indicated that defecation and ambulation in the open field are unrelated. He questioned whether ambulation is a useful measure of emotionality in the rat.

Low correlations were found between day-one activity scores and the activity scores for the rest of the testing period (Whimbey & Denenberg, 1967). A high positive correlation was found between day-one activity and defecation from day two onwards. They conclude that day-one activity measures something different from the other scores. They maintain that

exploration and emotional reactivity emerge as two distinct factors. The level of exploratory drive of an animal and emotional reactivity are not different ends of the same continuum, but appear to be two independent factors, either or both of which may motivate the animal in a novel environment. This concept of exploratory behaviour being a motivational force was not new. It had previously been mentioned in the literature (Evans & Hunt, 1942) but this was the most definitive statement of the roles played by these variables in the behaviour of the animal in the open field.

3.1.2 The validity of measures of emotionality

Although ambulation has been taken as a case in point, similar confusion surrounds the other variables used in the open field. Indeed, the questionable validity of the open field as a measure of emotionality is reflected in Hall's statement that:

If it be granted that abstinence from eating is a measure of the rat's emotionality, then it may be said that defecation and urination are also adequate measures of individual differences in emotional behaviour. (Hall, 1934, p.396)

If it is not granted that failure to eat is an adequate indication of emotionality; that this is not, in Hall's terms, a blocking of behaviour by the animal's state of emotionality, then the concept of emotionality loses its force and defecation becomes merely another behavioural dimension of the open field that is consistent, but

meaningless. Furthermore, few studies have been done to investigate the relationship between defecation and failure to eat. In other words, the correlation between failure to eat and defecation had been replicated and confirmed many times, but nothing more than face-validity had been shown to exist between emotionality and the measures used. It is not inconceivable that any animal fails to eat in brightly lit conditions. Some studies in which sound and light levels had been varied (Broadhurst, 1957) indicated that there may be a relationship between defecation and fearfulness because defecation varied with the levels of sound and light.

Two methods are usually regarded as being indicative of the validity of a measure in the open field. As the animals are repeatedly exposed to the open field the situation becomes less threatening and the defecation response diminishes. Thus, as the emotional responses evoked by the open field diminish, so non-emotional responses increase. It was in this way that Hall (1934), relating defecation to eating in the open field, suggested defecation as a valid measure of emotionality.

The second procedure used in the validation of open field measures is the manipulation of stimulus conditions. Measures indicative of emotionality should increase as the stimuli (usually light or noise) are increased. There is confusion regarding the interaction of these variables. Some

experimenters have found that an increase in the light levels causes an increase in urination and defecation (Evans & Hunt, 1942), while others have found that light has no effect, but that an increase in the sound level caused these measures to increase (Broadhurst, 1957).

Estimating validity is usually difficult, largely because there are no external criteria against which to validate a given measure. A number of methods of validation of defecation and ambulation have been used. One of the more common procedures is to use correlation between measures. Usually, if an open field measure correlates with defecation it is accepted that it measures similar features of behaviour as defecation. This approach, however, has limitations. In the first place the validity of defecation is pre-supposed; secondly, correlations which have been reported are low and inconsistent between studies. It is therefore difficult to predict reliably the outcome in any given sample. (Ivinskis, 1970, p.175)

Ivinskis used three methods in an attempt to determine the validity of the responses measured. These were an examination of the decrease of defecation over time, a retest after time and stimulus variation. Results indicated that repeated exposure to the open field showed a general decrease in behaviour over days. Retest results obtained also showed a decrease in open field scores which indicates that open field experiences are remembered by the animals for considerable periods of time. This adaptation response limits the number of times that the open field can be used without adaptation interfering with the experimental treatment. In fact, one of the groups showed such a marked adaptation response in Ivinskis's retest that an increase in stimulus intensity did not evoke an emotional response.

of the same continuum of behaviour. Yet it had already been shown that the relationship between ambulation and defecation is not clearly understood.

3.2 Problem solving ability

3.2.1 The Hebb-Williams test

Another requirement for the estimation of the effects of an enriched environment on laboratory animals was the development of a test of intelligence and in 1946 Hebb and Williams published their method of rating animal intelligence. This intelligence test is an adaptation of a maze learning procedure. The start and goal boxes are placed at opposite ends of a closed field. The rat was accustomed to the field prior to the first trial. Movable barriers were then introduced into the field to produce a simple variable maze, to which the animal was again accustomed. None of the maze problems presented in the training period were the same as the test problems. Hebb and Williams claimed that, the method minimised variations attributable to motivation and gave a score that was based on a large number of performance trials.

The results of the Hebb-Williams closed field test indicate that animal scores increase with the animal's age, and although the statistics are not significant there are

indications of reliability in that the animals retested showed differences that were not nullified by repeated test experience. Furthermore, they argued that such differences should disappear with repeated exposure to the test situation if they were caused either by timidity or by the animal being able to learn more quickly. Higher test scores may be the result of a better capacity for perceptual discrimination or may be the result of certain animals having a better memory of the preceding tests than others. The reason memory may have been a factor in the closed field was because Hebb and Williams used the first trial as habituation and discarded the results. The following two trials on the series were used as scoring. The original Hebb-Williams test comprised 12 problems (see Appendix 1) presented to each animal three times. The first presentation of the problems was also for habituation, and the remaining two trials were used as test trials.

Whether the performance differential is due to memory is not material, because memory is an intellectual function and not a function of training in the Hebb-Williams test. Timidity was not a variable since the animals were not tested until all signs of timidity had disappeared. Also, as a result of the adaptation trials the animals exhibited no signs of exploratory behaviour, and all animals went directly to the goal. There was no indication that the animal was not eager for food, or that a low scorer was tending to follow the

walls. Nor was any overt behaviour observed as being the cause of individual differences.

Rabinovich and Rosvold (1951) extended and developed the Hebb-Williams test. They used a different set of problems with six preliminary problems for adaptation. These problems were used in the present study (see Appendix 2). Rabinovich and Rosvold showed that the test adequately discriminated animals reared in an enriched environment from animals with brain lesions and normals. Retest reliability was high. They wrote:

It should be noted that the closed field test described in this paper bases its quantitative score on qualitative analyses of performance on twelve different tasks. This is a deliberate attempt to evaluate rat intelligence as a more general and integrated phenomenon that has been done in the past, and in this way to accomplish the measurement of a capacity in the rat which more closely approaches our concept of intelligence in man. (Rabinovich & Rosvold, 1951, p.128)

3.2.2 The problem of motivation

It could be argued that the individual differences shown by the Hebb-Williams CF test were not indicative of intelligence but were, in fact, differences in motivational level. This concept derives from the Yerkes-Dodson law. If the tasks were graded in difficulty, the optimum level of motivation would have varied inversely with task difficulty. Although the motivation to complete the tasks was the same throughout (23

hours starvation) the Yerkes-Dodson law states that the motivation relative to each task will vary, accounting for the score variation of the items.

One argument against this application of the Yerkes-Dodson law was the implication of a level of performance on each task beyond which, due to motivation not being optimal, animals were incapable of achieving. Such a level was not reported in the literature. Furthermore the law was later repealed (Brown, 1965), but not before the Hebb-Williams test had been adapted for water escape motivation (Rosvold & Mirsky, 1951). This adaptation to water escape motivation was necessary for another reason; a second criticism of the Hebb-Williams test was that although the starvation period was the same, animals may be differently motivated to run to food.

3.2.3 The adaptation to water escape

In the modified Hebb-Williams closed field test the animals were required to swim from one side of a water tank to the other. The dimensions of the Hebb-Williams floor test were unchanged. The start and goal boxes were in diagonally opposite corners and movable barriers could be placed in the water to create a variable pattern maze.

This adaptation of the test had far reaching effects on

investigations of behaviour after enrichment. In order to make the animal run to food, the animal has to be deprived of food. The question arises of whether or not this is detrimental to the enrichment process. The feeling was that food deprivation would be more detrimental to an environmentally enriched animal than to an environmentally deprived animal. Although this would partially destroy results and differences would be greater than already indicated, the possibility of deprivational or motivational causes for the differences had to be eliminated. Thus the adaptation to water escape motivation was welcomed as a means whereby these possible causes of differences could be eliminated.

Once again the animals were adapted to the testing situation by repeated exposure prior to the experimental trials. Results showed that the water test was a reliable indicator of differences between treated and untreated animals, and also indicated that the animals required about 44 days of training on the water test before it became a reliable measure of group differences.

Rosvold and Mirsky (1954) had found the reliability of the first test low in comparison to the second, which led them to believe that 44 days of training were necessary to make the water test reliable. It was later shown that a 44 day training was not necessary: that the water test is reliable

even when the training was considerably shorter (Vasiljkovitch, 1973), and that the low reliability may have been the result of the technique of running trials on the floor and water test alternately and not to the water test as such (Rosvold & Peters, 1954). Rosvold and Peters (1954) used the same system of training, but did not intersperse the floor test. They tested both the reliability of the water test and whether the test would adequately discriminate between electrically shocked and normal animals, and whether increased motivation for food would affect the animals' performance.

Results indicated that the water test discriminated between the shocked and normal groups. The test did not differentiate between animals that were food deprived only. It was also shown that more practice was needed in the water test than in the floor test for comparable reliability.

It is evident, too, that the increased motivation for food (increased food deprivation) does not improve the rat's performance in the water test, thus justifying the assumption in the first paper (Rosvold and Mirsky)...It is, in fact, sufficiently impaired to make the food deprived group indistinguishable from the electroconvulsed group with respect to error decrease...However, it is clear that the performance of a rat in an escape situation is disturbed by increasing motivation for food. Therefore, it is not appropriate to use the water test as a measure of the effect of a treatment on intelligence, unless it can first be shown that the treatment does not affect motivation for food. (Rosvold & Peters, 1954, p.145)

The development of both the open field test and the modified Hebb-Williams water maze played a large part in the research

directed towards the effect of early experiences on the behaviour of animals. They provided the means whereby the effects of such manipulation could be measured. Without these measures it is doubtful whether Hebb's original discovery would have led to the present status of the effects of early environmental enrichment.

3.2.4 A re-examination of the problem of validity

In the light of research on environmental effects on humans (Child, 1974; Clarke, 1968; Gray & Klaus, 1965), it is clear that the enrichment process causes major changes in the abilities of the human organism. With animals it is also accepted that there occurs a major change in behaviour as a result of the enrichment process.

The tests used in the determination of the enrichment effects are of questionable validity. The validation of Hall's procedure rests upon the work of Ivinskis (1970), whose major contribution was stimulus variation, and upon a comment by Hall (1934) that high stress in humans causes an involuntary evacuation due to the action of the sacro-illiac system, which may also be expected in rats. Unfortunately, even in the area of stimulus variation there has been considerable contradictory evidence (Broadhurst, 1957). In spite of this, the open field and Hebb-Williams tests were used in this study, not because they are necessarily testing emotionality

and problem solving ability, but because they are relatively stable indicators of the effects of enrichment. The measurement of enrichment effects is therefore relative to the deprived groups rather than to any absolute reference point. The problem of the validity of the tests as measures of behavioural dimensions is therefore not relevant to their use in this study.

4 THE EXPERIMENT

4.1 Rationale

From the discussion presented in the previous chapter it may be seen that many studies were designed to test the gains of the animal in adulthood subsequent to exposure to enriched environments during the first ten days of life. This presupposed that the gains made by the animal are, if not permanent, at least of a long term nature (Denenberg, Woodcock & Rosenberg, (1968). There was also the realization that adult behaviour of the animal could be altered by the application of stimuli during the youth of the animal. It was therefore not unreasonable to enquire whether adult behaviour could be moulded, or perhaps controlled, by the type and duration of stimuli presented in youth.

Researchers were able to show that when genetic differences had been controlled by random allocation to experimental groups, differential early stimuli caused considerable differences between the groups (Denenberg, Karas, Rosenberg & Schell, 1961; Denenberg & Whimbey, 1968; Whimbey & Denenberg, 1966).

Studies relating to human development have tended to concentrate on two aspects of the research mentioned: the permanence of early environmental effects or the reversibility of the effects of early deprivation. Clarke (1968) maintained that the early enrichment of animals was by no means permanent, and that from the welter of scientific data very little could be extracted to show that the gains were permanent. He indicated that imprinting, thought to be a permanent process, decays rapidly until, after 21 days, there remain only residual effects. He wrote that work by Harlow which indicated a long-term effect on maternal behaviour of monkeys, also showed that maternal behaviour improved with subsequent births, and suggested that, unless early behaviour is reinforced it is quickly extinguished and the gains made by the animal in youth are lost. Clarke argued that the enrichment of animals need not take place only at an early age in order to be effective, but that, although an animal is deprived in early life, the effects are not irreversible. He wrote:

A few researchers, however (e.g. Woods, 1959) report that a later enriched environment can markedly reduce the effects of early sensory or motor deprivation, and, as noted, even the Harlow experiment using extreme and prolonged isolation of unmothered monkeys shows a later spontaneous shift in the degree of damage. (Clarke, 1968, p.1063)

Animal research thus provided the mainspring for a closer look at human development, and Clarke summarised the differences between the two sides by postulating that the

animal's reactions were the result of deprivation at an early age, rather than enrichment.

Denenberg (1969) supported this hypothesis, citing results by Cooper and Zubeck who bred maze-bright and maze-dull animals through 13 generations. These animals were then reared in normal, enriched and restricted environments before being tested on the Hebb-Williams test. The results were:

	Normal Environment	Enriched Environment	Restricted Environment
Maze-Bright rats	117,0	111,2	169,7
Maze-dull rats	164,0	119,7	169,5

Looking first at animals reared in the normal environment, we see that the usual differences between maze-bright and maze-dull animals are obtained, with the bright animals making 117 errors on the average over the 12 problems and the dull animals making 164 errors. When both groups are reared in an enriched environment, the reduction in the number of errors for the bright animals is negligible, but the reduction in errors for the dull group is considerable - to the point where the difference between the groups is no longer significant. However, the consequences of rearing in a restricted environment are that both groups have approximately 170 errors. The restricted condition had a deleterious effect upon the maze-bright rats, but an insignificant effect on the maze-dull animals (Denenberg, 1969, p.33).

The differences between the environmentally enriched groups were only as much as the differences gained by selected breeding for 13 generations. This may argue that the effects of environment are somewhat more potent than those of genetic selection, but this is a nature-nurture argument and outside the scope of this study.

Notwithstanding this support of Clarke's hypothesis Denenberg argued that the effects of early stimulation were long-term and possibly affected subsequent generations of animals which had been stimulated in early life. In support of his hypothesis Denenberg cited a number of studies across species (from monkey to man) which all indicated that early experience had a profound effect on later behaviour.

Yet Clarke's hypothesis is not without support from other sources. Harlow (1948) had postulated the formation of learning "sets" which had enabled the animal to learn learning skills; that is to learn to generalise rather than to learn specific behaviours or responses to problems. Harlow thought that this learning could take place at any time during the development of the animal. Harlow typically used adult monkeys in the development of the hypothesis.

Other support comes from studies concerned with human development. Gray and Klaus (1965) for example reported significant gains made by children involved in an intervention programme for culturally deprived children. The programme was to offset the progressive retardation observed in schooling of culturally deprived children. The children were given experiences designed to develop and reinforce attitudes towards high-school achievement. Language and intelligence tests showed improvement on test scores for the experimental group and losses on the scores for members of

the control group.

Similarly, a study by Child (1974) indicated that mildly subnormal children showed considerable gains when treated in an enriched environment, suggesting that the severe conditions of an institution for the mentally subnormal could be overcome by the effects of enrichment, and that this could be done at adulthood indicating that age is not a significant parameter of the enrichment process.

It is thus suggested that there is currently a very considerable over-emphasis on the role of early experience, and that reinforcement or non-reinforcement over long periods may be the more important variable. (Clarke, 1968, p.1069)

4.2 Aim.

Clarke argued that "a later enriched environment can markedly reduce the effects of early sensory or motor deprivation" (1968, p.1063). which generated the primary aim of the study reported in this thesis; to examine the effects of the duration of early deprivation on the behaviour of laboratory animals. More specifically, the intention was to investigate whether the effects of prolonged deprivation on the behaviour of laboratory animals was reversible, and whether longer deprivation periods were more detrimental to the animal than shorter periods, in terms of the animal's ability to recover after enrichment.

Thus, if groups of animals matched for age are deprived for different lengths of time, the differences between the control and experimental groups for each age group will not vary significantly. By examining the animals at different ages the validity of Clarke's argument, that is that longer periods of deprivation do not prevent recovery from the deprivation effects could be tested experimentally.

The length of time in the enrichment field was determined by considerations of the Grassroots study already mentioned. One week in the life span of the rat approximated the six month enrichment period used by the Grassroots study, both being approximately 0,7 percent of total life span. It had been shown that periods of mild enrichment as short as five days were almost as effective as longer periods of ten and twenty five days (King, 1958), and it was felt that the enrichment of seven days would be adequate. This short enrichment period, also enabled an examination of the results for determining the existence of a critical period for development in the rat.

4.2.1 Hypothesis

On the basis of the previous discussion it can be stated that the gain in performance is independent of the age at which enrichment commences. For testing purposes this will mean that the differences between the mean scores for experimental

groups of animals entering the enriched environment at four different ages (ages: 23 days, 30 days, 37 days and 44 days) and control groups will not vary significantly.

4.2.2 Research design

It was thought that a matched group design would facilitate the examination of Clarke's hypothesis. The difference between experimental groups and their respective controls for different periods of deprivation would give an indication of whether long periods of deprivation were more damaging to the animal than short periods of deprivation. This difference would also give an indication of whether animals would enrich equally well as they matured. If animals do not enrich equally well, it is an indication that a critical period for enrichment exists, which is influencing the enrichment process. and will also be contradictory evidence to Clarke's hypothesis.

Each experimental group was introduced into the enriched environment at a different age, and all the experimental groups remained in the enriched environment for 7 days. (See figure 1)

The first group (E1) was entered into the enriched environment at 23 days of age and remained in the environment until 30 days old. The second group (E2) of experimental

Figure 1. Research design

groups	treatment	rest	open field	rest	Hebb- Williams
$E_1 C_1$	23 - 30	31	32 - 37	38	39 - 44
$E_2 C_2$	30 - 37	38	39 - 44	45	46 - 51
$E_3 C_3$	37 - 44	45	46 - 51	52	53 - 58
$E_4 C_4$	44 - 51	52	53 - 58	59	60 - 65

animals were entered into the enriched environment at 30 days, and remained until 37 days, the third group (E3) was entered at 37 days and remained until 44 days and the final group (E4) was entered into the enriched environment at 44 days and remained until 51 days. After enrichment the groups were removed from the enriched environment and tested with their controls (C1, C2, C3, C4), which were the same age. Each group had to have its own control group as the effects of increasing age on performance were unknown.

4.3 A pilot study

A pilot study was conducted with two specific aims. First, to ascertain the requirements of the environment for enriching the animals. Secondly, to ascertain the earliest time at which the animals could be introduced into the environment. Accordingly, an enriched environment was derived from descriptions in the literature (e.g. Forgays & Forgays, 1952; Forgas, 1955) and playthings such as tunnels, pyramids and see-saws were introduced into the environment. The cage used for the enriched environment in the pilot study had the same dimensions as the cage used in the main study. This apparatus is more fully described in the following section.

It was originally hoped that the first experimental group would open its eyes on the enriched environment, and the animals were introduced into the environment at the age of 14

days, before their eyes opened. In order to prevent maternal deprivation in the pre-weaned pups, the mother was placed in the cage with the litter. This was found to be unsatisfactory, however, as the mother made a nest in the corner of the cage and ventured out only to eat. The pups were immediately brought back by the mother if they left the nest. By the 21st day only the more adventurous of the animals were leaving the nest. It was therefore decided to begin the enrichment period at 23 days, after weaning, thereby avoiding possible contamination by maternal deprivation.

It was still necessary to determine whether the environment was rich enough to significantly affect test performance of animals and the animals were left in the environment, without the mother, for a further seven days. It was felt that the previous enrichment effect would be comparatively small compared with the effect of the following seven days when the animals were locomoting freely.

When the animals were 30 days old they were removed from the environment and tested on the modified Hebb-Williams test for problem solving and on the open field test for emotionality. The procedure used in the administration of these tests will be discussed in section 4.6. On neither of these tests was the variance between experimental and control groups large enough to be meaningful, nor was a trend detected. It was

therefore decided that the environment was not rich enough to trigger the process, and steps were taken to enrich it substantially, by the introduction of additional playthings. This subsequent environment will be discussed in the next section.

4.4 Apparatus

Three items of apparatus were used in the experiment: the apparatus for enriching the environment, the apparatus for testing problem solving ability and that for testing emotionality.

4.4.1 The enrichment apparatus

The enrichment cage was 70 X 70 X 70 cms in size with aluminium walls and a stainless steel wire mesh floor. The cage was supported 8 cms above the floor by legs which allowed a tray to be slid under the wire mesh floor to collect excreta. This facilitated cleaning without disturbing the environment. The walls of the cage were painted bright red, blue, green and yellow. A red platform, approximately 30 cms wide and raised 25 cms from the floor, was placed against three sides of the cage.

On the floor of the cage was placed a Habitrail. This commercially produced device was designed to provide an

enriched environment for hamsters. It consisted of three chambers of different sizes interconnected by yellow perspex tunnels. The tunnels were ridged on the inside to allow foothold so that animals could climb vertically. The chambers were also made of yellow perspex, and the largest contained a big, red running wheel. This largest of the chambers gave access, by means of tunnels, to the two smaller chambers and was itself accessed by a short tunnel from the floor of the cage. The smaller of the two chambers was situated vertically above the running wheel arena and contained food. This chamber could also be accessed by a slightly sloping ladder leading to the raised platform. The larger of the two chambers was situated upon the platform and contained a device resembling a radar dish made of red perspex. The dish was centrally pivoted and, being able to revolve, served a similar function to a running wheel. An exit from this chamber led directly to the platform which was connected to the floor of the cage by means of a ladder. On the platform was situated another running wheel of blue plastic. The diameter of the tunnels was small enough to enable a young rat to climb vertically and large enough not to impede the passage of a full-grown animal. Miscellaneous items such as mirrors, bells and tunnels were also in the cage. Food and water were distributed throughout the cage, and a tray containing wood shavings was placed underneath the raised platform.

4.4.2 The open field apparatus

The open field consisted of a circular field 1,68 m in diameter surrounded by an aluminium wall 61 cms high, painted gloss black. The floor of the open field was white formica and was divided into segments by black lines painted on the surface. The segments were made up as follows: an inner circle with a diameter of 63 cms was concentric with the circumference of the open field. Six equally spaced radial lines further divided the open field into segments to enable measurement of the ambulation of the animal.

Light was provided by a single unshaded 100 w frosted electric lamp suspended 52 cms above the centre of the open field.

4.4.3 Problem solving apparatus

The Hebb-Williams test was a 76 cm square tank, 30 cms deep. The tank was constructed of galvanised iron with a start and goal box in diagonally opposite corners. The tank was filled with water to a depth of 20 cms by means of a hose from a nearby tap. The water was heated to 23 degrees Celsius, and kept as close to this temperature as possible throughout the testing. The tank water was regularly changed with the aid of a water pump.

The goal box was elevated above the water level and was accessed by means of a ladder sloping at an angle of approximately 15 degrees to the floor of the tank. The floor of the tank was divided into 36 squares, each 12,5 cms square to demarcate placement of the barriers and the recording of a subject's path during testing. Barriers made of galvanised sheeting were 30 cms high (the same height as the walls of the tank) and varying lengths, each a multiple of 12,5 cms so that the barriers could be placed exactly on the lines between the squares.

The lid of the tank was of clear perspex and hinged so that it could be raised to position the barriers. The start box lid was independent of the tank covering and hinged so that the animal could be placed in the start box without disturbing the rest of the tank. It was noted in the pilot study that the rats tended to cling to the tops of the barriers if the top was open, and all testing was therefore conducted with the top closed.

4.5 Sample design and size

The subjects were 48 male albino rats bred from randomly selected females in the rat colony at the Department of Psychology, University of Cape Town. Female albino rats were mated and placed in cages with dimensions 17 X 28 X 12 cms. The cages were covered with wire mesh tops through which food

pellets and water were provided ad-lib. The floor of the cages was covered with wood shavings which was changed periodically. The cages were housed in the temperature (21 degrees Celsius) controlled rat colony. The colony had a controlled 06h00 to 18h00 light-dark cycle.

The birth dates of the litters were recorded and the animals were not disturbed until weaning at 21 days. At weaning all animals were sexed and separated from littermates. It was decided not to use females in the experiment for three reasons. First, it has been shown that sex differences exist in the open field test (Broadhurst, 1957) and it was thought that such differences may contaminate the variables. Secondly, the estrous cycle was a potential source of difference. Finally, to avoid animals not being able to complete the training or testing because of pregnancy, only males were used in the experiment.

For each of the four experimental and control groups 12 male rats were selected by means of the split-litter technique. In other words, each group of 12 animals was made up of rats from at least two different litters born within 24 hours. This group was then randomly assigned to an experimental or control group, each group thus containing six animals. All the litters used in this study were born within five days.

There were four experimental and four control groups. Each

experimental group was matched to a control group for age. This was to control for ageing factors which may have confounded the enrichment process. Genetic factors were randomized by the split-litter technique. It was intended that each group contain 10 subjects, but the housing of 80 animals was impractical in terms of the space available in the rat colony. It was therefore decided to reduce the number of subjects in each group to six, making a total of 48 rats, which could more easily be maintained. While this reduced the probability of statistically significant results it was, in retrospect, a good move because the testing of 12 animals on the open field and Hebb-Williams simultaneously stretched the capacities of both tests and teams to the limit.

4.6 Procedure

As with the apparatus, the procedure is properly divided into three sections relating to the three major aspects of the experiment. Prior to a detailed examination of these individual procedures some aspects of the overall procedure will be examined. After weaning, sexing, and allocation to experimental and control groups the experimental groups were removed to the test rooms where they were housed in similar cages to those in which they had been reared. During the move the cages were covered to keep visual stimulation of the animal to a minimum. While in the treatment rooms the experimental groups also received minimal visual stimulation.

To do this the cages were placed in larger aluminium boxes, open at the tops so that the animals were not light deprived. The conditions of the treatment room were as nearly identical to that of the colony room as possible: Both were temperature controlled (21 degrees Celsius), both had 06h00 to 18h00 time-switch controlled light-dark cycles and both had an effective white-noise substitute in the form of the air-conditioner.

The control groups were housed in the colony in similar cages to those in which they had been reared, and here too stimulation was kept to a minimum. At the appropriate testing time the cage (also covered) was removed to the treatment rooms where it remained until testing was completed. The testing procedure for both groups was identical on the open field and the Hebb-Williams tests. The animals were identified by rings on their tails.

At the appropriate time each experimental group was entered into the enriched environment. After enrichment the animals were rested for one day before being tested with their controls on the open field. After they had completed testing both groups were again rested for one day and then tested on the Hebb-Williams apparatus. After testing, all animals were removed to the rat colony. Both rooms in which the open field and Hebb-Williams test were housed were also temperature controlled at 21 degrees Celsius and had a white-noise

substitute provided by air-conditioning units.

Before and during the experiment it was necessary to clean the rat cages. This was done at weekly intervals with a minimum of handling.

4.6.1 The enrichment procedure

At the appropriate time each group of animals was introduced into the enrichment cage where they remained for seven days and nights. During this time the animals were handled daily. Each animal received 50 back strokes from the base of the skull to the base of the tail. After handling the animals were placed back in the enrichment cage.

4.6.2 The open field procedure

Both the experimental and control groups were brought into the test room in their cages. A rat was chosen and placed in the centre of the open field. All rats were placed in the field facing in the same direction. All animals were given six trials on six successive days. Each trial consisted of two, two-minute exposures to the open field, making a total of four minutes per trial. Testing was carried out each day between 18h00 and 21h00. The time of testing was kept as constant as possible in order to eliminate possible variation due to the general activity level of the animal which varies

as a function of the sleep-wake cycle of the animal.

Variables recorded during the open field trials were

(a) Defecation: the number of boluses eliminated by the animal during the four minute trial.

(b) Ambulation: the number of times an animal crossed a segment boundary was recorded and indicated the level of ambulation.

(c) Rearing: the number of times an animal stood on its hind legs supported by its tail.

(d) Grooming: the number of times the animal scratched, washed its face or licked its fur.

(e) Latency: the time in seconds before the animal moved out of the inner circle.

These variables were recorded by two experimenters and when differences were found the mean score was taken for the trial. It was decided to use grooming as a measure of emotionality rather than urination for two reasons. First, there is some confusion as to whether the frequency or quantity of urine is important in the evaluation of emotionality (Pare, 1964). Secondly, it was decided to attempt to verify whether grooming correlated highly with defecation (Radloff, 1959). The other measures were standard.

The boluses were removed and the walls and floor of the field thoroughly cleaned with a solution of Tepol detergent and

water after each trial. The field was allowed to dry before the next trial.

4.6.3 The Hebb-Williams procedure

Both control and experimental groups were brought to the test room in their cages and again a temporary cage was used to house each animal until the group had been tested, when all animals were returned to the home-cage. The testing of the subjects on the Hebb-Williams was similar to the procedure reported by Rosvold and Mirsky (1954). Practical considerations forced a modification of presentation of the problems and scoring procedures. Two practice or test problems were presented each day instead of only one, thereby halving the testing time and avoiding overlap of groups during testing.

Instead of the scoring system proposed by Rosvold and Mirsky, which was a composite of time and the number of error zones entered, the system proposed by Pollard and Simpson (1961) was used. Pollard and Simpson suggested that the best performance on any one trial was obtained if the animal swam directly from the start to the goal box. They believed that the number of squares entered on any one trial was a good indicator of the performance; the fewer squares entered, the more direct the route taken from start to goal box. This method was used for scoring of the Hebb-Williams test.

Before each subject was given any practice problems it was first accustomed to the water tank. This consisted of placing the animal at the start box, facing the goal box, and releasing it to swim to the goal box. During accustomization there were no barriers in the tank and on the first few trials the animal was guided to the goal box. After the trial, the animal was removed from the goal box and placed in the drying cage. This was a cardboard shoe box with crumpled newspapers on the floor, a grid roof and an electric hairdryer positioned in such a way that a jet of warm air was directed into the drying cage. This was a fast and efficient method of drying the animal.

A subject was deemed accustomed when it swam directly from the start to the goal box on five consecutive trials without circling, retracing its path or swimming along the walls of the tank.

When accustomed, the subjects were presented with six practice problems, two on each day. Each practice problem consisted of eight consecutive trials on that problem, with a one minute break between trials. For a diagram of the problems, see Appendix 3.

After the animals had finished the practice problems they were presented with the test problems (see Appendix 2). The method of presentation of these problems was the same as for

practice problems. The time in seconds, taken by the animal to reach the goal box, as well as the number of squares entered, was recorded. Time was measured from the moment the subject left the start box to when its front paws touched the ladder leading to the goal box. Each subject therefore had two measures for each problem, the measures being the mean of eight trials in each case.

5 RESULTS

The open field test provided five measures of emotionality and the Hebb-Williams test two measures of problem-solving ability. The mean scores of the experimental and control groups on the five variables of the open field test, are presented in Table 1 and the mean scores of the experimental and control groups on the Hebb-Williams test are shown in Table 2. Raw data can be found in Appendix 4.

In each case the difference scores between the experimental and control groups were determined, and a oneway analysis of variance for a fixed effects model was carried out to determine whether these differences between the four experimental groups and their controls were statistically significant.

It was decided to use a one way analysis of variance on the difference scores for two reasons. Firstly, the interaction effect score of a two way ANOVA will be composed of both the effects of age at enrichment and the effects of age at testing. This makes a two way ANOVA an inappropriate statistical tool because only the age at enrichment and not the age at testing is of importance to the study. Secondly,

Table 1

Mean scores on the open field test

Groups	Defecation	Grooming	Rearing	Ambulation	Latency
Experimental					
E1	3,72	2,05	7,33	41,9	3,85
E2	2,82	1,30	7,55	36,28	3,33
E3	3,02	1,88	5,85	34,45	5,75
E4	2,62	1,25	5,43	19,58	5,80
Control					
C1	5,07	3,18	6,47	27,45	5,13
C2	4,80	2,85	5,50	21,12	5,60
C3	7,97	4,53	4,18	10,80	8,27
C4	6,15	2,48	4,65	15,75	6,87

Table 2

Mean scores on the Hebb-Williams test

Groups	Time (secs.)	Squares
Experimental		
E1	10,27	15,85
E2	11,40	16,34
E3	11,51	16,13
E4	12,39	- 15,91
Control		
C1	12,92	16,48
C2	12,68	16,66
C3	13,05	16,61
C4	13,80	16,62

it has been noted

that the repeated measures ANOVA does not yield additional information beyond that which can be obtained from a simpler analysis of gain scores. And since the former approach is potentially confusing and in some cases controversial, while the latter approach is straight-forward and easy to follow, there is much to recommend the gain score approach to the data analysis (Huck & McLean, 1975, p.516).

Where these differences were significant, an a posteriori test for the comparison of all possible pairs of means was undertaken. The procedure used was the Student-Newman-Keuls (SNK) because it is robust under conditions of non-normality and heterogeneity of variance, and because it does not require a significant F to indicate differences between means. The test is also sensitive without being prone to type II error (Kirk, 1968).

The Bartlett-Box (Kirk, 1968) test was then used to determine the homogeneity of variance between the groups.

The groups used in the experiment were small and it was not thought necessary to set the rejection level high to avoid chance-large factors. Furthermore, because the group size is

small, the probability of a type II error is increased with high rejection levels. To offset these factors the rejection level was set at 5 percent.

5.1 Results on the open field test

For the sake of clarity, each of the variables will be dealt with separately.

5.1.1 Defecation

Figure 2 is a graphical representation of the relationship between the experimental and control groups. It can be seen that for groups 1 and 2 the differences appear to be stable, but for groups 3 and 4 the differences increased considerably. Mean group differences can be seen in Table 3, and show the total mean of -2,95 with a standard deviation of 1,84. The variance table for defecation (Table 4) shows that these differences are significantly different from what can be attributed to chance. The observed F of 10,07 with three and twenty degrees of freedom is considerably greater than is required to reject the null hypothesis of no difference between the means at the 1 percent level ($p < 0,01$).

The SNK procedure indicates two homogeneous subsets of groups which have means that do not differ by more than the shortest significant range. The first subset contains groups 3 and 4

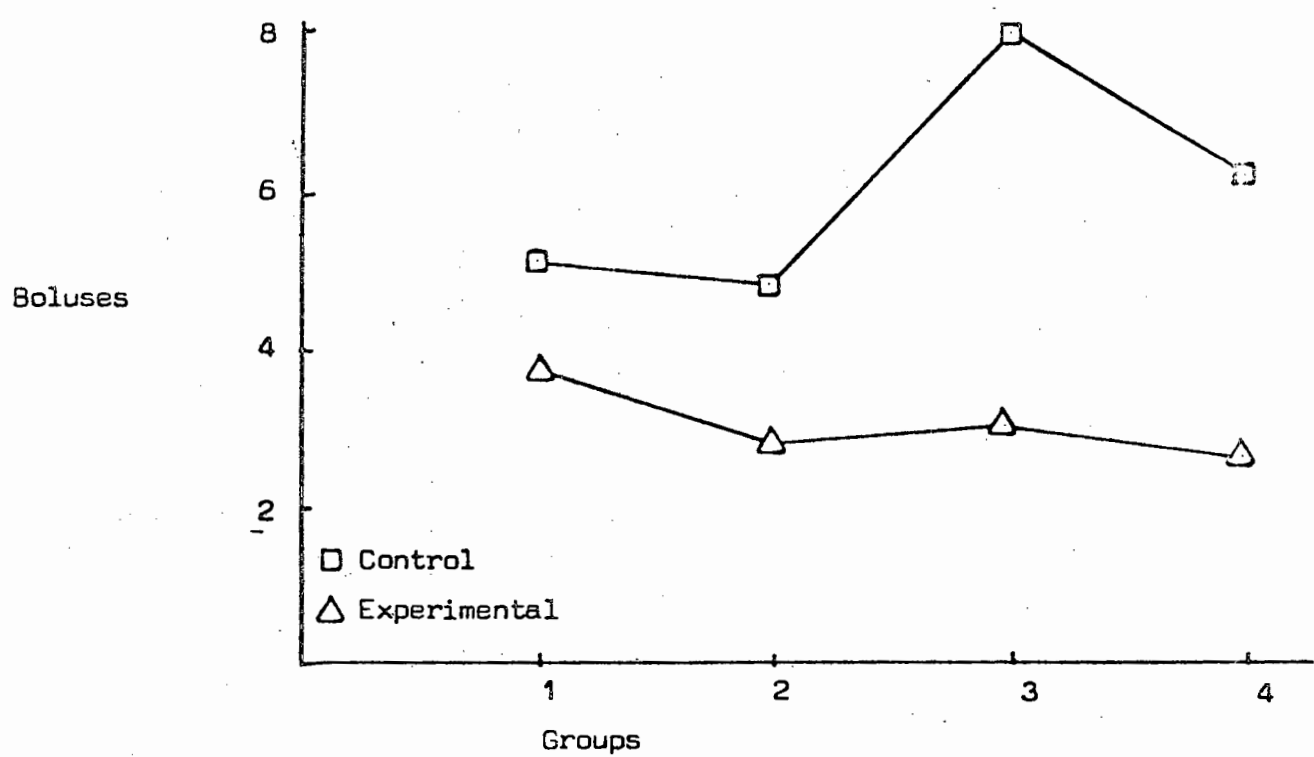


Figure 2 Mean scores for defecation

Table 3

Experimental minus control group differences for defecation

Group	Mean	Standard deviation	N
1	-1,35	2,09	6
2	-1,98	0,40	6
3	-4,95	0,92	6
4	-3,53	0,93	6
Total	-2,95	1,84	24

Table 4
Variance table for defecation

Source	Sum of squares	df	Variance estimate	F	p
Between	47,01	3	15,67	10,07	0,01
Within	31,13	20	1,56		
Total	78,14	23			

and the second subset contains groups 1 and 2. Groups 3 and 4 therefore differ significantly and groups 1 and 2 also differ significantly with a minimum range of 2,95 ($p < 0,05$).

The Bartlett-Box test for homogeneity was then applied and an observed F of 3,82 with three and twenty degrees of freedom was found to be significant at the 1 percent level. The null hypothesis that the groups have been drawn from a population having different variance could not be rejected. The variances between the groups may be heterogeneous and the significance of the mean difference scores cannot be attributed to the treatment alone.

5.1.2 Grooming

Figure 3 represents the relationship between the experimental and control groups, and shows how the groups vary together. Mean group differences centre at -1,64 with a standard deviation of 1,14, as shown in Table 5. Group 3 again shows a larger variation from the total mean.

It is shown by Table 6, the variance table for grooming, that the difference is not significant with an observed F of 2,73 ($p = 0,07$). The null hypothesis of no difference between the means can therefore not be rejected.

The Bartlett-Box test for homogeneity for variance showed an

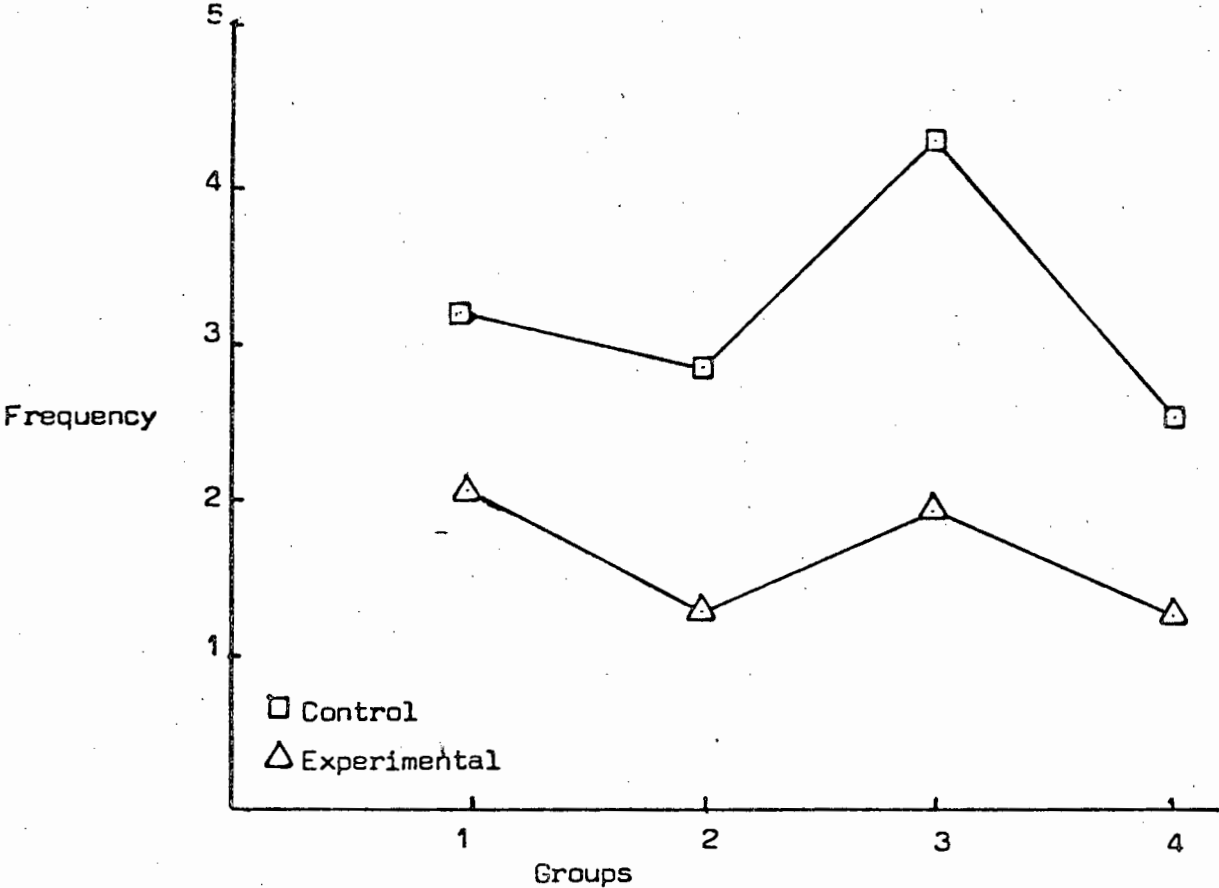


Figure 3 Mean scores for grooming

Table 5

Experimental minus control group differences for grooming

Group	Mean	Standard deviation	N
1	-1,13	1,33	6
2	-1,55	0,63	6
3	-2,65	1,23	6
4	-1,23	0,75	6
Total	-1,64	1,14	24

Table 6
Variance table for grooming

Source	Sum of squares	df	Variance estimate	F	p
Between	8,70	3	2,90	2,73	0,07
Within	21,22	20	1,06		
Total	29,92	23			

F of 1,17 which is not significant ($p=0,32$). The null hypothesis that the groups have different variances is rejected and it may be accepted that the groups have been drawn from populations with homogeneous variance.

A correlation was computed between grooming and defecation scores in an attempt to verify Radloff's (1959) claim of high correlation between such scores. The observed r was 0,20. It is possible, however, that the coefficient is low because the variance was not attributable to treatment alone, as was indicated by the Bartlett-Box test for homogeneity of variance.

5.1.3 Rearing

Rearing scores for the experimental and control groups appear to co-vary in the same manner as the grooming scores. This is shown in Figure 4. The mean experimental and control group differences are shown in Table 7. Group mean variance about the total mean of 1,34 are smaller than for the previous two variables, while the standard deviation is a good deal larger.

The variance table indicates that the differences between the group means for rearing is not significant. The observed F is 0,25 ($p=0,62$), and the null hypothesis of no differences between means cannot be rejected.

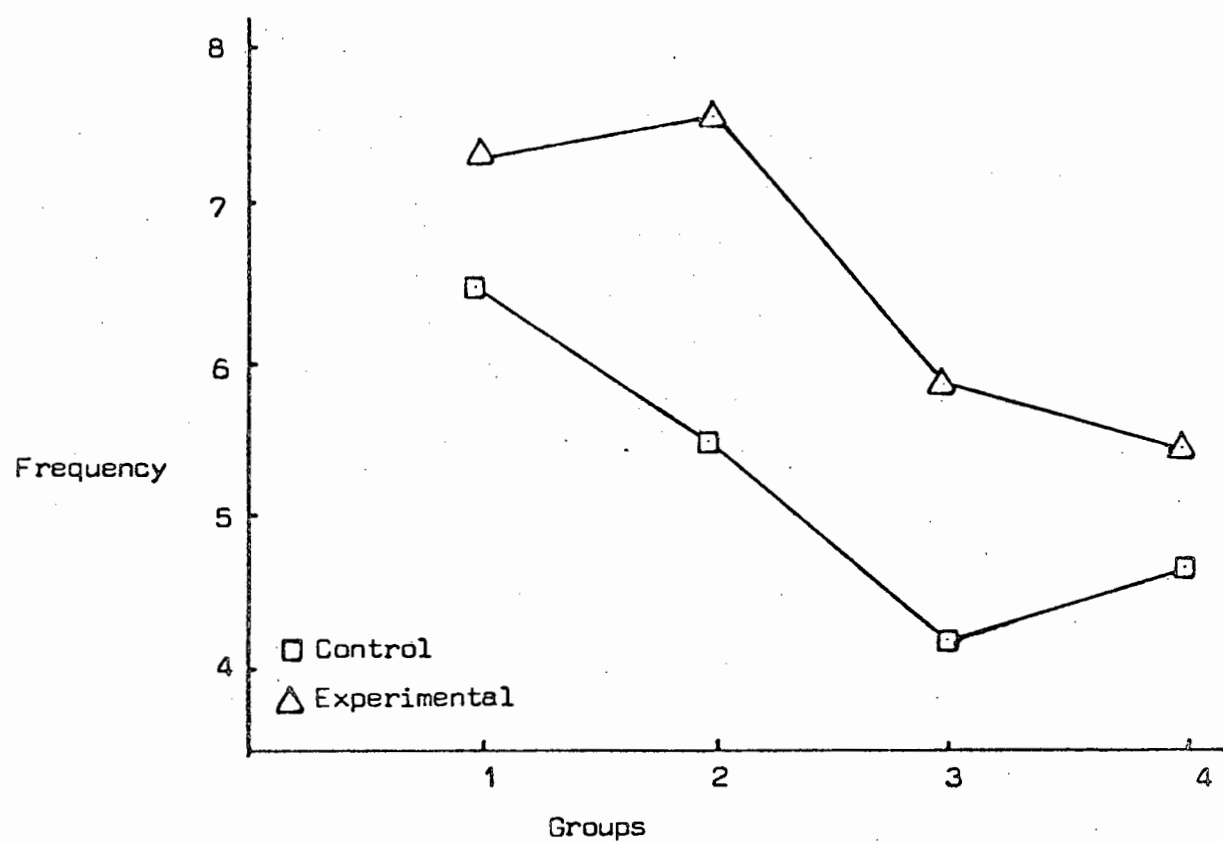


Figure 4 Mean scores for rearing

Table 7

Experimental minus control group differences for rearing

Group	Mean	Standard deviation	N
1	0,87	2,17	6
2	2,05	3,37	6
3	1,67	2,34	6
4	0,78	3,88	6
Total	1,34	2,87	24

Table 8

Variance table for rearing

Source	Sum of squares	df	Variance estimate	F	p
Between	6,87	3	2,29	0,25	0,62
Within	183,15	20	9,16		
Total	190,02	23			

The Bartlett-Box test shows an observed F of 0,72 which is not significant ($p=0,55$). The null hypothesis is rejected, indicating that the samples originate from populations with the same variance.

5.1.4 Ambulation

Ambulation scores are represented in Figure 5, showing the effects of age on ambulation in the open field. As the animal gets older, there is a marked decrease in the tendency to locomote for both control and experimental groups. The mean differences between the groups are shown in Table 9. The variation from the total mean is small for groups 1 and 2, and is considerably above the total mean for groups 3 and 4.

The variance table for ambulation, (Table 10) indicates that these differences are not significant with an observed F of 1,47 ($p=0,25$). The null hypothesis of no differences between means cannot be rejected.

The Bartlett-Box test gave an observed F of 3,89 which is a good deal more than is needed for significance at the 5 percent level ($p<0,01$). The null hypothesis of no differences between the variance is rejected and the variance of the samples is not homogeneous.

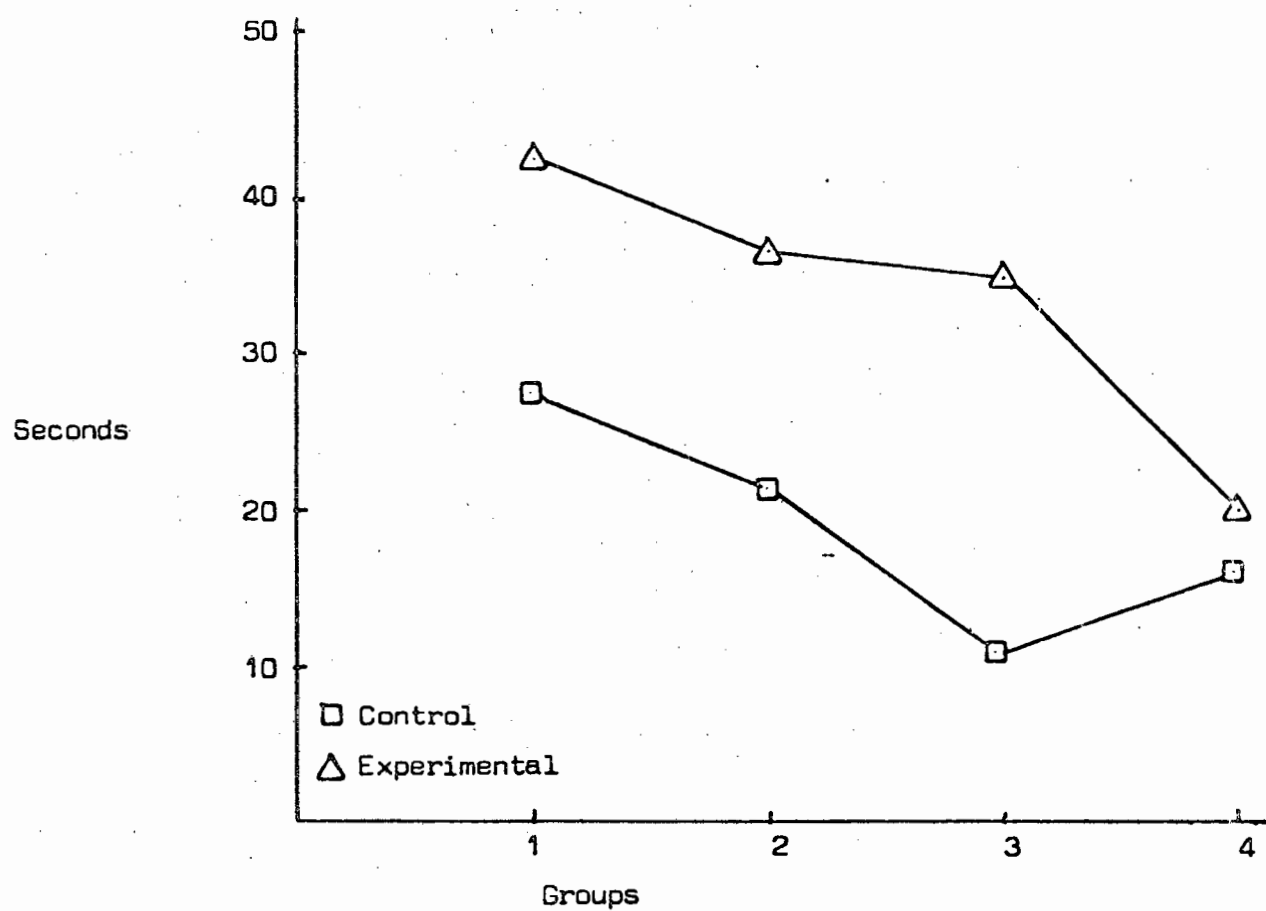


Figure 5 Mean scores for ambulation

Table 9

Experimental minus control group differences for ambulation

Group	Mean	Standard deviation	N
1	14,45	22,69	6
2	15,17	21,05	6
3	23,65	4,43	6
4	3,83	9,78	6
Total	14,28	16,88	24

Table 10

Variance table for ambulation

Source	Sum of squares	df	Variance estimate	F	p
Between	1186,47	3	395,49	1,47	0,25
Within	5367,81	20	268,39		
Total	6554,28	23			

5.1.5 Latency

Figure 6 shows the control and experimental group scores for latency. It is evident that the animals tend to stay in the centre of the field for longer as they get older. This is not as marked as the decrease of ambulation scores over time. The tendency for older animals to be cautious and locomote less is supported by Figure 6. This tendency can be seen in Table 11, which shows the mean experimental and control group differences for latency.

Table 12, the variance table for data relating to latency shows that the differences between the groups is not significant. For an observed F of 0,29, $p=0,66$ which indicates that the null hypothesis of no differences between the means cannot be rejected.

The Bartlett-Box test gave an observed F of 0,89 and this is not significant at the 5 percent level ($p=0,45$). The null hypothesis of different variances between the samples is rejected.

5.2 Results on the Hebb-Williams test

The statistical procedures used for the analysis of the Hebb-Williams data were identical to those used on the open field data. Once again, for the sake of clarity, the two

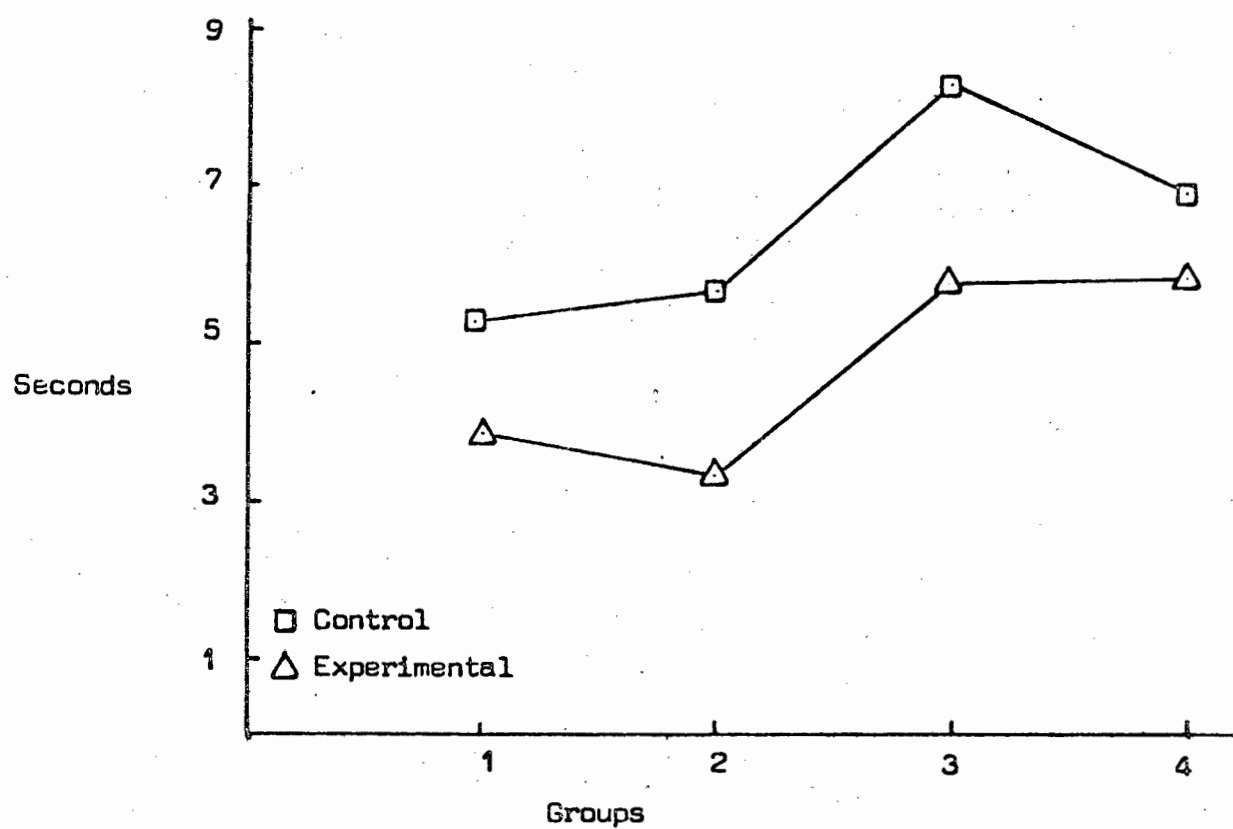


Figure 6 Mean scores for latency

Table 11

Experimental minus control group differences for latency

Group	Mean	Standard deviation	N
1	-1,28	4,62	6
2	-2,27	2,72	6
3	-2,52	2,39	6
4	-1,07	2,73	6
Total	-1.78	3,08	24

Table 12

Variance table for latency

Source	Sum of squares	df	Variance estimate	F	p
Between	9,21	3	3,07	0,29	0,66
Within	209,36	20	10,47		
Total	218,57	23			

variables used in the Hebb-Williams test will be discussed separately.

5.2.1 Time scores on the Hebb-Williams test

The relationship between the experimental and control group scores for the mean time taken is shown in in Figure 7. It is evident that groups 2, 3 and 4 have approximately equal differences, but the difference between, E1 and C1 is somewhat greater than the differences between the other groups. Table 13 shows the mean group differences.

It can be seen from the variance table for the time scores, Table 14, that this difference is not significant with an observed F of 0,48 ($p=0,67$). The null hypothesis of no difference between the means cannot be rejected.

The Bartlett-Box test shows an observed F of 4,84 which is significant at the 1 percent level ($p=0,01$). The null hypothesis of no differences between the variances is rejected.

5.2.2 Squares scores on the Hebb-Williams test

The relationship between the experimental and control groups for the squares scores on the Hebb-Williams test is shown in Figure 8. It is evident from this figure that there is little

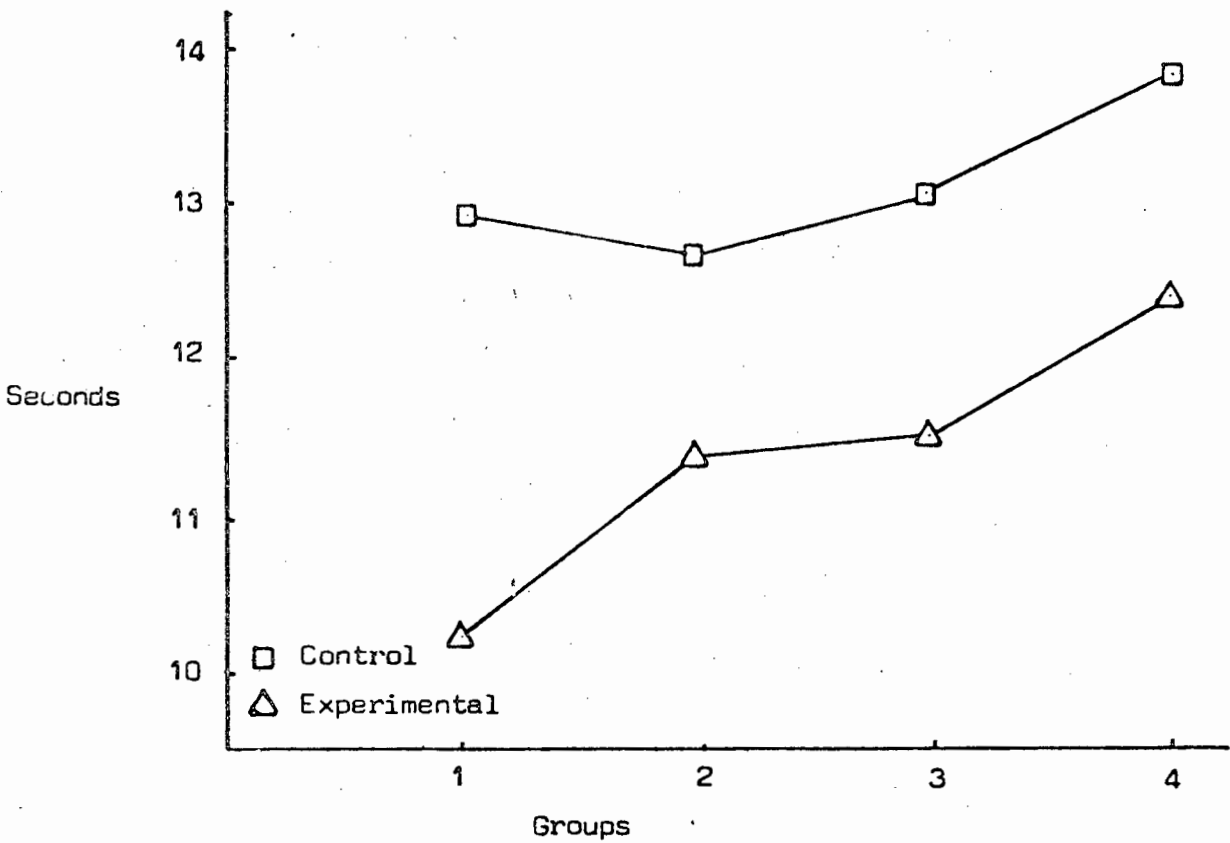


Figure 7 Mean time for Hebb-Williams

Table 13

Experimental minus control group differences for time

Group	Mean	Standard deviation	N
1	-2,65	4,01	12
2	-1,28	2,51	12
3	-1,54	3,91	12
4	-1,41	1,23	12
Total	-1,72	3,08	48

Table 14
Variance table for time

Source	Sum of squares	df	Variance estimate	F	p
Between	14,18	3	4,73	0,48	0,67
Within	430,77	44	9,79		
Total	444,95	47			

variation between the means of the groups. This can be more readily seen in Table 15, which gives the mean group differences.

Table 16, the variance table for the difference scores for squares shows that the mean group difference scores are not significantly different with an observed F of 0,04 ($p=0,09$). The null hypothesis of no difference between the means cannot be rejected.

The Bartlett-Box test shows an observed F of 1,43 which is not significant ($p=0,23$), and the null hypothesis of no difference in the variance is not rejected.

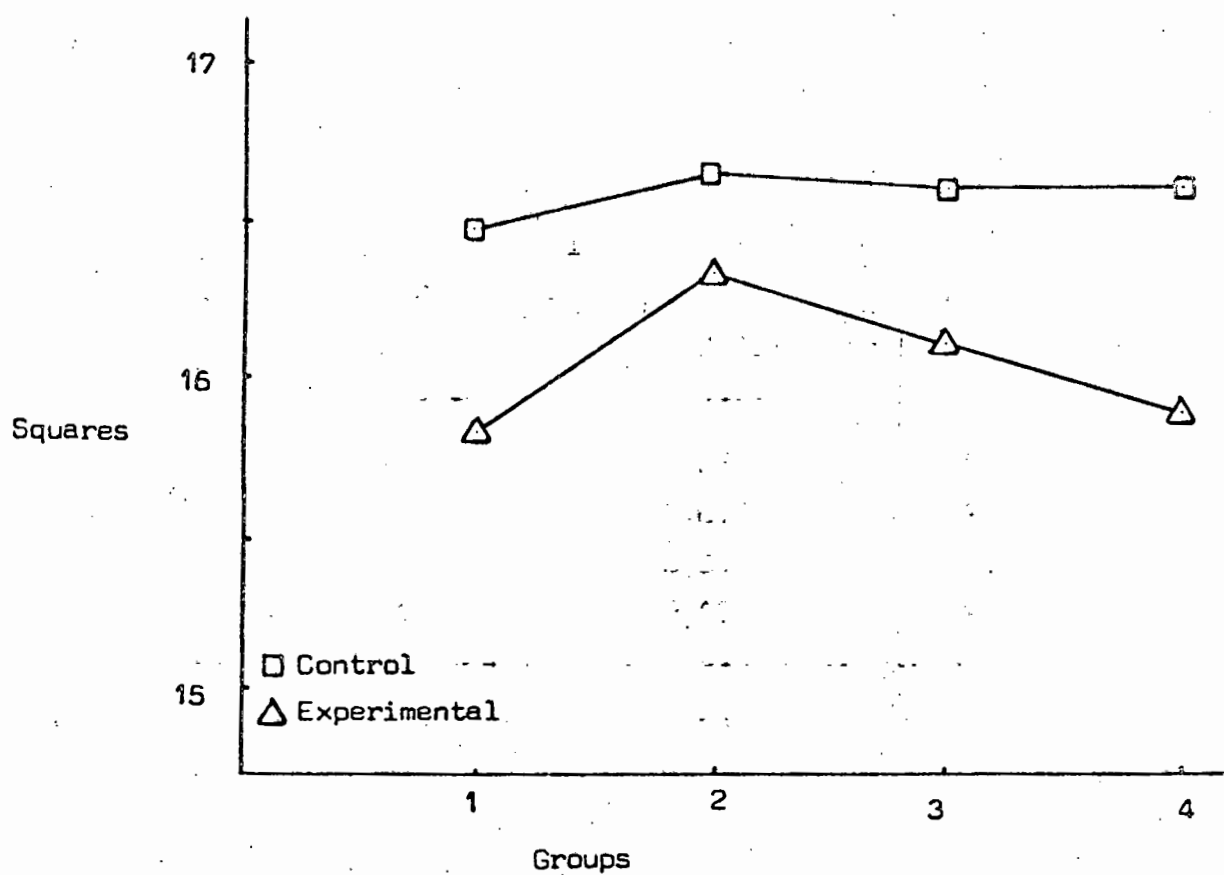


Figure 8 Mean error for Hebb-Williams

Table 16
Variance table for squares

Source	Sum of squares	df	Variance estimate	F	p
Between	1,04	3	0,35	0,04	0,09
Within	410,29	44	9,32		
Total	411,33	47			

6 DISCUSSION OF RESULTS

Once again, for the sake of clarity, the open field and the Hebb-Williams will be treated separately.

6.1 Discussion of the open field results

The results of the open field test show that, in the main, the differences between the control and experimental groups are not significantly different. The alternative that there would be differences between the groups could not be accepted, and Clarke's hypothesis that increasing deprivation is not a criterion of the animal's ability to recover from being deprived is supported. This is illustrated by the fact that in the present study, the experimental animals gained in performance over the control animals to the same degree after varying periods of deprivation.

With the exception of defecation, the results of the open field experiment supported Clarke's hypothesis. Although the mean group difference scores for defecation were significantly different, the Bartlett-Box test cast doubt on these results, on account of the lack of homogeneity of the variances of the groups. Although robust under conditions of

non-normality and heterogeneity of variance the analysis of variance is suspect under extremes of these conditions, and a Bartlett-Box F of 3,82 ($p=0,01$) can be considered an extreme condition. It can therefore not be accepted without the constraint that the present findings represent real differences in defecation scores of animals belonging to different groups.

There are two possible reasons for the heterogeneity of variance between the groups on defecation scores. First, this could be because of a failure of the split-litter technique to randomize genetic differences between the groups. This, however, appears unlikely, because such genetic differences would probably have been reflected in the other variables. The Bartlett-Box test would have shown that the variances were heterogeneous in the other groups.

The fact that the Bartlett-Box test showed heterogeneity of variance for ambulation holds the clue for the other possible reason for heterogeneity of variance in defecation scores. It has been reported that age has an effect on ambulation, causing animals to locomote less as they get older (Furchtgott, Wechkin, & Dees, 1961). This effect can clearly be seen in Figure 4. Thus the age of animal may be a parameter affecting both defecation and ambulation scores, and may have been the cause of the significant statistic produced by the Bartlett-Box test when applied to defecation

scores.

The implication of this is that animal defecation varies as a function of age as well as emotionality, which throws some doubt on the validity of defecation as a measure of emotionality in the open field.

There is, however, a third possible reason for the heterogeneity of variance in defecation. Examination of the group mean differences for ambulation (Figure 5), defecation (Figure 2) and grooming (Figure 3) shows that the differences for group 3 are all a good deal greater than the other groups. This may be because of some unknown maturational factor in the animal's development. It should be noted that group 3 were entered into the enrichment cage and testing began on day 45. The open field test continued for six days and the animals were 51 days old at the end of this period. This is about the time of onset of puberty in the animals, which may have been maturational effect that affected the scores for these groups.

Several factors work against this as a possible explanation. First, group 4 testing began at day 52 and continued until the animal was 58 days old. This was also through the pubertal period of the animal, and it may be expected that the maturation effect would have been present in the fourth group as well. Examination of Figures 2, 5, and 6, however

indicates that there was, if anything, a recovery from the extremes of variance exhibited in group 3.

Secondly, the other variables for group 3, rearing, and latency, did not show any of the effects recorded for ambulation, defecation, and grooming. This is the more suprising because of the relationship between latency and ambulation. It appears likely that the maturation effect of puberty should also have appeared in these groups, particularly as the groups are related.

Finally, the Bartlett-Box test for grooming did not indicate that the variance for this variable was heterogeneous, and if grooming was closely allied to ambulation and defecation by virtue of the maturation effect, then it too should have had a significant Bartlett-Box test result.

By the same criterion, when the SNK results are examined, defecation stands alone. There were no significant differences for either ambulation or grooming scores while for defecation scores differences between the subsets containing groups 1 and 2, and groups 3 and 4. This suggests some contamination of the defecation scores. Yet, the experimental treatment for all groups was the same and it is difficult to imagine a contaminating factor that affected only one of the groups. Furthermore, the effect cannot be due to experimenter bias, because, while the trials were not run

blind, both the open field and the Hebb-Williams were run with two experimenters to record results. A schedule rotating the experimenters was strictly adhered to. It may be more parsimonious to postulate that age is a parameter of defecation.

6.2 Discussion of the Hebb-Williams test result

Neither of the variables used on the Hebb-Williams test showed significant differences scores. Clarke's hypothesis is therefore supported by these results on the Hebb-Williams test, and it would appear that the problem-solving ability of the animals was not affected by increasing periods of deprivation.

It is worth noting that the Bartlett-Box test result for the time scores is significant at beyond the $p=0.01$, indicating that the group variances were heterogeneous. It has been suggested that age was the probable factor causing the heterogeneity of variance, but the Bartlett-Box test findings casts some doubt on the matter.

On the open field variables the factor may be due to age because the variables are, relatively speaking, independent. On the Hebb-Williams test, however, the time and squares variables are related. It has already been mentioned that both variables measure the animals' problem-solving ability

and that as the animal enters more squares so also does his error score and the time which the animal will take to complete the trial increase. Yet the Bartlett-Box test result for the squares scores is not significant.

It appears likely that if the heterogeneity of variance was attributable to age then this factor would have affected a variable closely related to time taken on the Hebb-Williams trials. Yet the variance for the groups on the squares scores were homogeneous.

Other possible sources of variance, such as item difficulty, could not have contributed to the heterogeneity of variance because all items were equally difficult for all animals. Furthermore, this cannot explain why an animal scores low on a trial, but high on a subsequent trial. The source of the heterogeneity of variance is not known.

The fact that there were no significant differences across all the groups, or at least across all the variables on the open field and on the Hebb-Williams tests, indicates that no critical period influenced the treatment. It cannot be argued that a critical period exists for defecation alone because all the variables in the open field test purport to measure emotionality, and all the variables should show significant differences if a critical period for development was in effect. For the same reason, the significant differences of

the time scores on the Hebb-Williams test do not indicate the existence of a critical period. It would appear, therefore, that a critical period for behavioural development does not exist at the ages when the animals were enriched.

7 EVALUATION

Several criticisms can be levelled at the study. King (1958) for example wrote:

In experiments including more than one test, the tests usually follow each other instead of being given in a random order or such a systematic order as provided by a latin square. This multiple testing procedure raises the question of what effect prior tests have on subsequent ones. (p. 52)

This criticism applies to this experiment as the tests followed each other in a single standard procedure. It is felt, however, that this experiment was not concerned with the measurement of emotionality or problem solving behaviour in any absolute sense, but was concerned with the effects of enrichment and deprivation on groups relative to each other. As the testing procedure was the same for all groups, the effect of the sequence of testing would have been the same for all groups whether experimental or control, and the relative effect will be small.

Ideally the experiment should have varied both the time of entry into the enriched environment cage and also the length of enrichment so that the several age groups were enriched for different lengths of time. Unfortunately this was not practicable. It has already been mentioned that the

limitations of a single apparatus and few experimenters necessitated the doubling of frequency of presentation of problems. The resources of the team were stretched to the limits and any increase would have been impractical. For the same reasons it was impossible to run the trials blind and to assure a lack of experimenter bias.

Another criticism of the experiment is that the control animals should have been moved to the testing area at the same time as the experimental groups. The animals were, however, left in the colony until the time when they were to have been tested and were then moved. At the extremes an animal was moved at 21 days of age and 51 days of age, a difference of 30 days. This difference is considerable and may have caused some variation in control group scores. All the cages should have been moved at the same time.

It is worth mentioning again the need for a standard rather than a deprived environment in order that some measurement of the degree of deprivation is possible. Although most researchers seem to think that as long as the environment remains constant across all groups, it is of little concern. Without some systematic measurement of the degree of deprivation, however, the degree of enrichment cannot be determined, and the measurement of deprivation, without a base-line is difficult, even impossible.

8 CONCLUSION

Clarke (1968) stated

It has been my purpose to re-examine the common emphasis on the formative role of early experience, summarized typically and approvingly by Yarrow (1961), who states "the significance of early infantile experience for later development has been reiterated so frequently and so persistently that the general validity of this assertion is now almost unchallenged." (p. 1068).

In challenging the effect of early experience Clarke argued that reinforcement effects were the major parameter of the learning experience, not the age at which the experience occurred.

This investigation, aimed at determining the effects of prolonged periods of deprivation on animals, and specifically whether longer periods of early deprivation caused a decrease in the animals' ability to recover from this deprivation, examined Clarke's hypothesis.

Specifically, the study tested the hypothesis that the gain in performance is independent of the age at which enrichment commences. This hypothesis was not rejected, which indicates that the age at which enrichment occurs is not an important parameter in the enrichment process. This further indicates

that longer periods of deprivation do not materially affect the deprived animal, insofar as the difference scores were not statistically significant. This lends support to Clarke's hypothesis that early deprivation is reversible, and to the extension of the hypothesis that longer periods of deprivation do not have significantly long term effects.

The experiment also aimed at determining whether a critical period existed for the enrichment of animals between the ages of 23 and 51 days. No evidence of the existence of a critical period for behavioural development was found, and it is assumed that the critical periods for enrichment are not operable in the age range used in this study.

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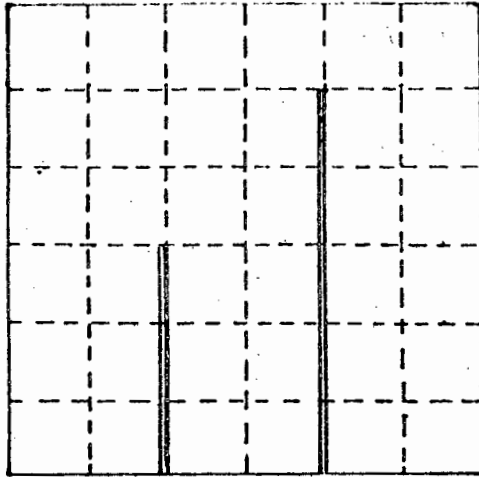
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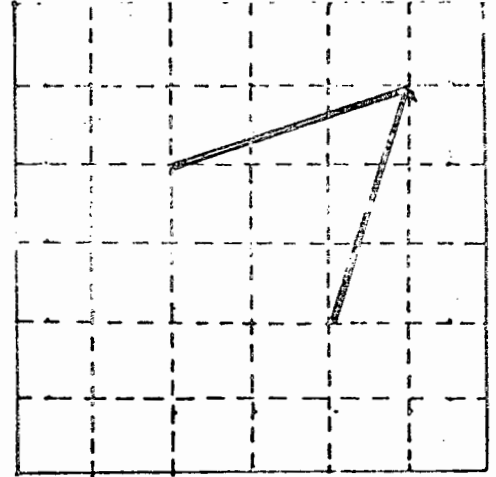
Problems used in the Hebb-Williams test

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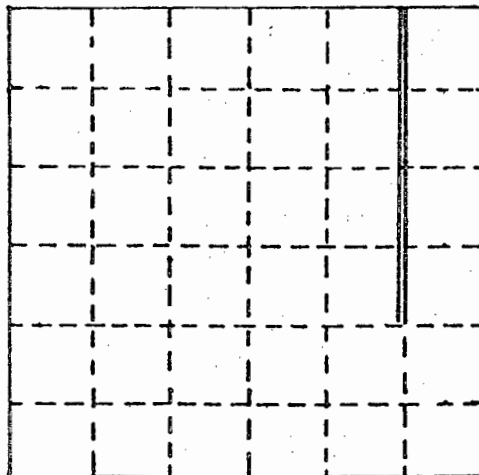
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Problem 1



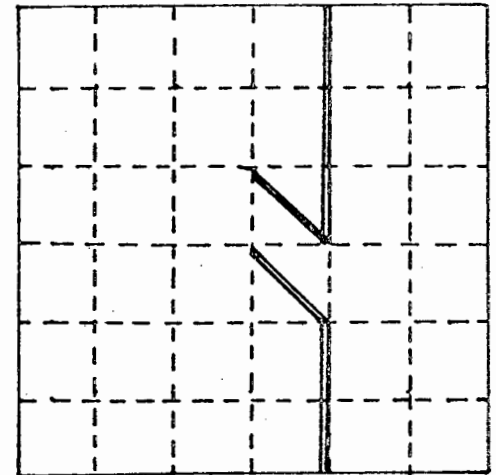
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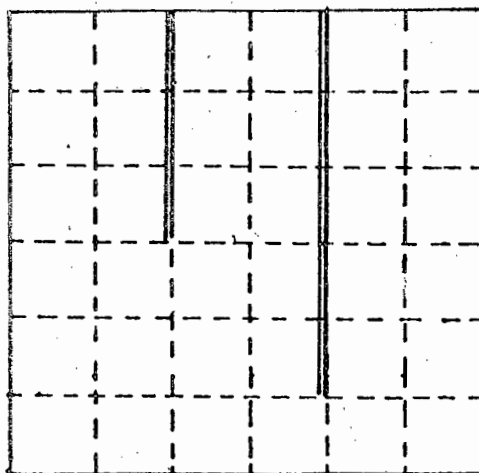
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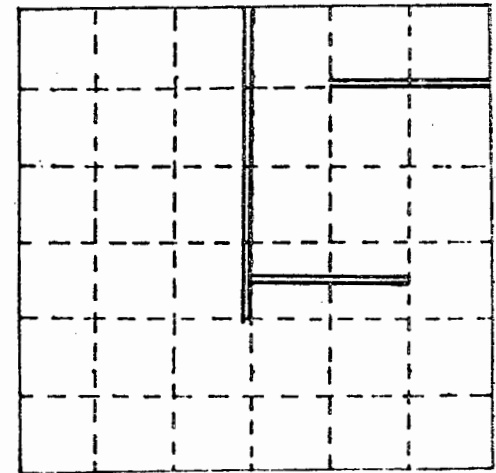
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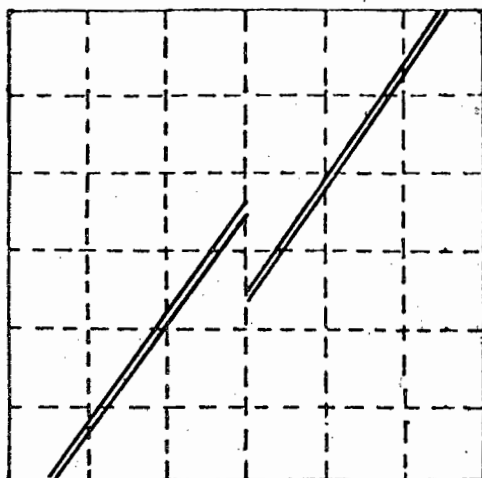
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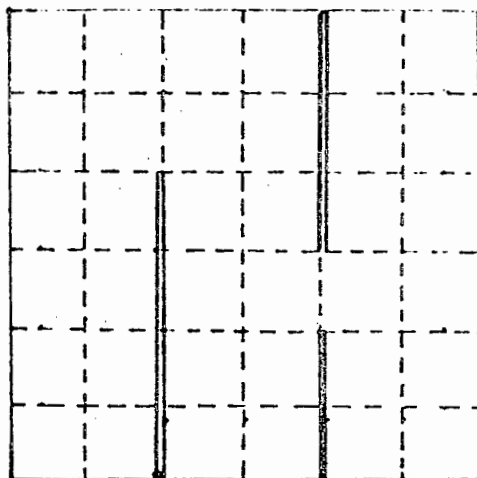
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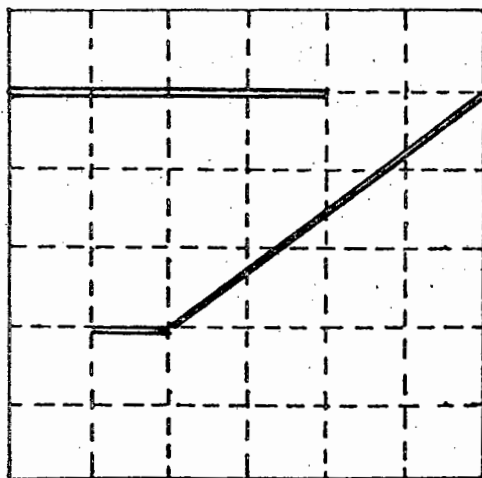
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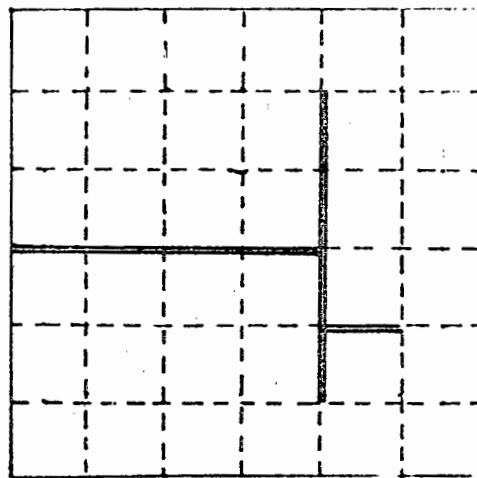
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Problem 8



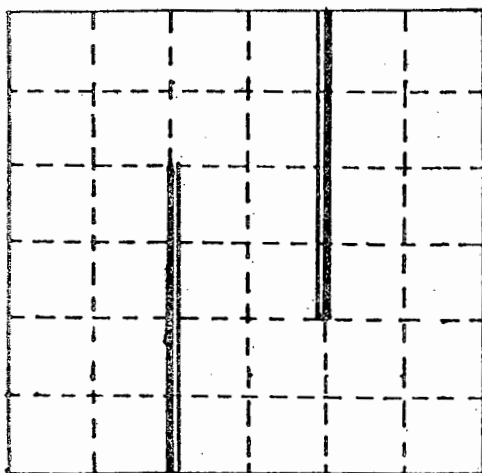
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Problem 9



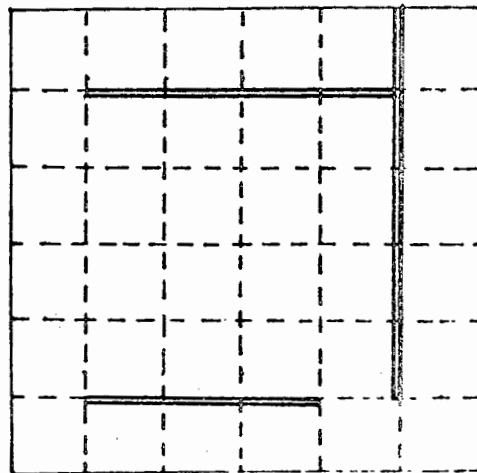
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Problem 10



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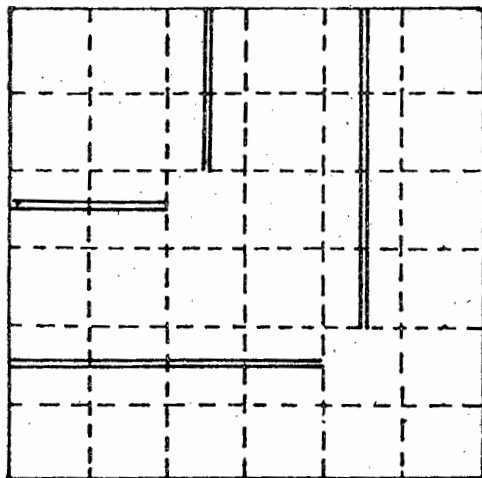
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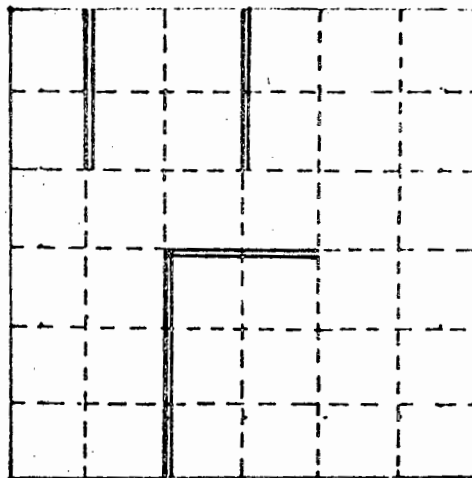
Problem 12

Problems used in the Hebb-Williams water maze



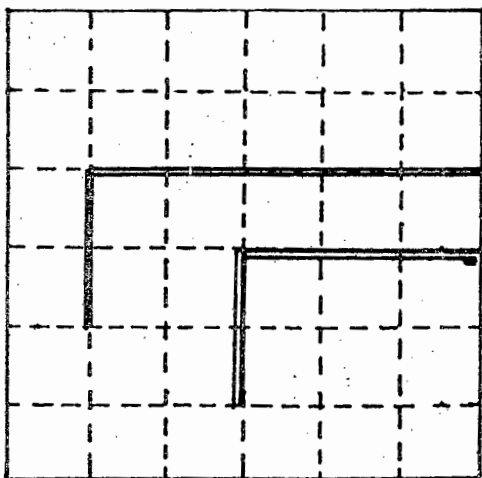
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Problem 1



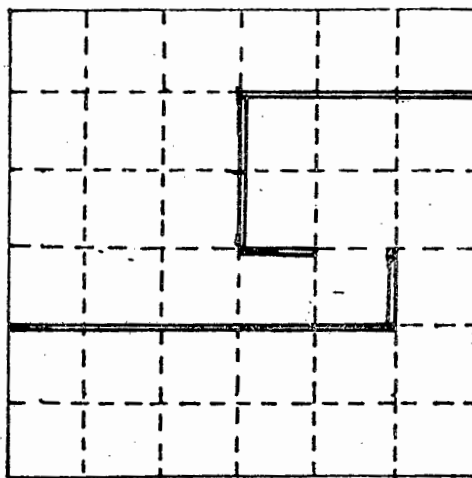
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Problem 2



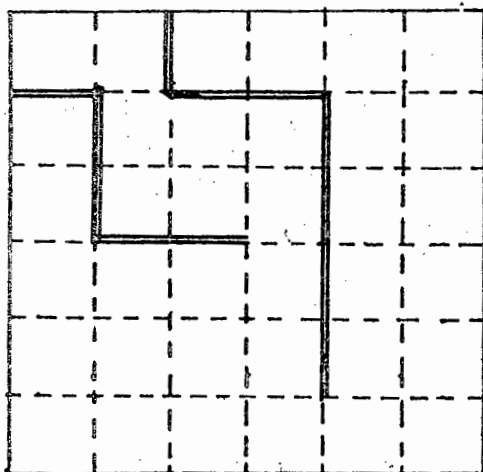
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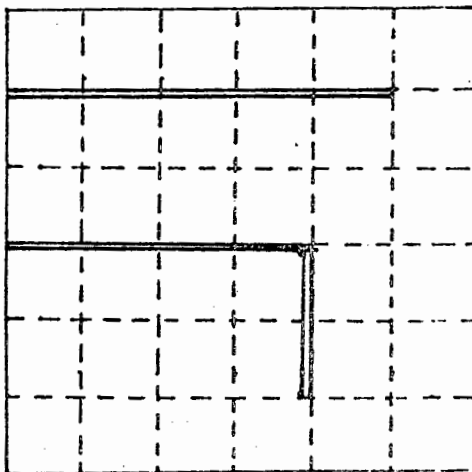
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Problem 4



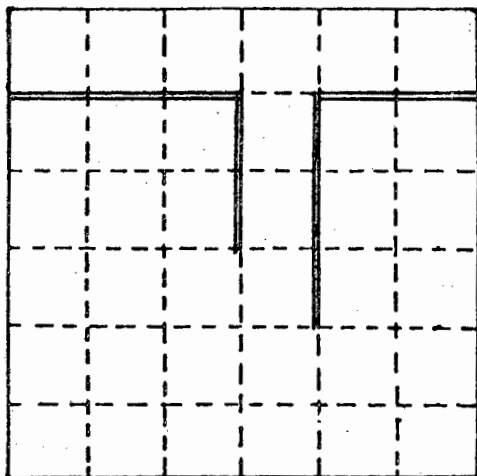
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Problem 5



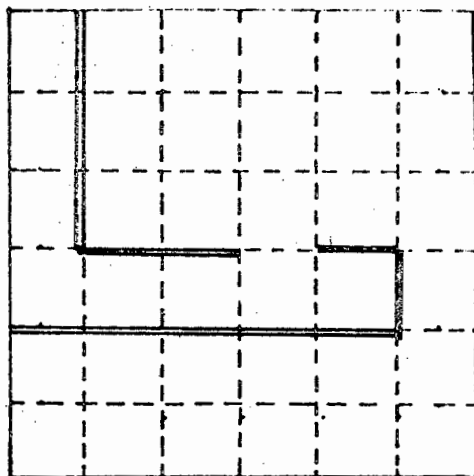
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Problem 6



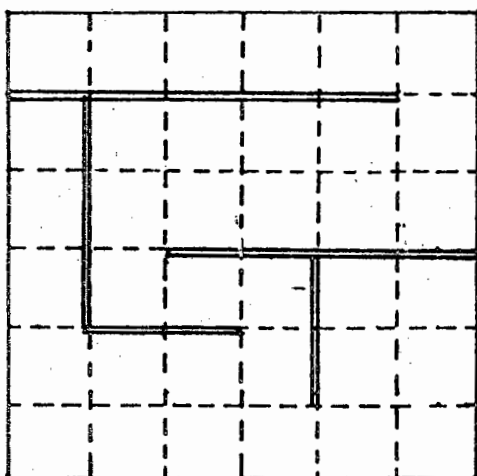
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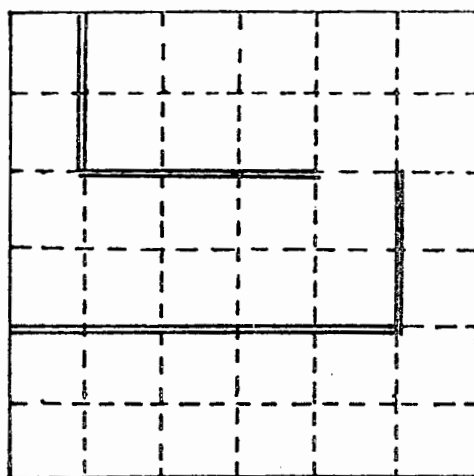
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Problem 8



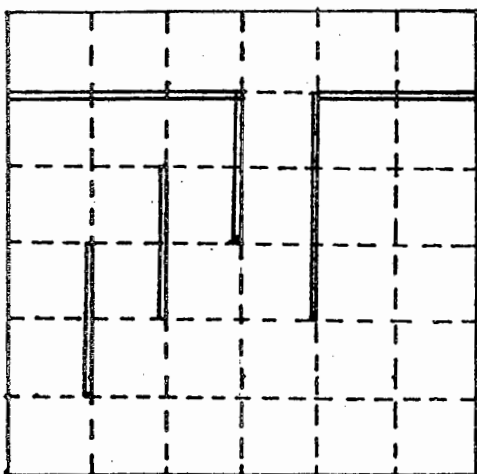
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Problem 9



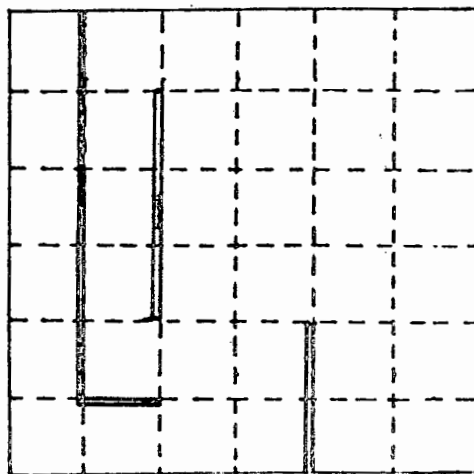
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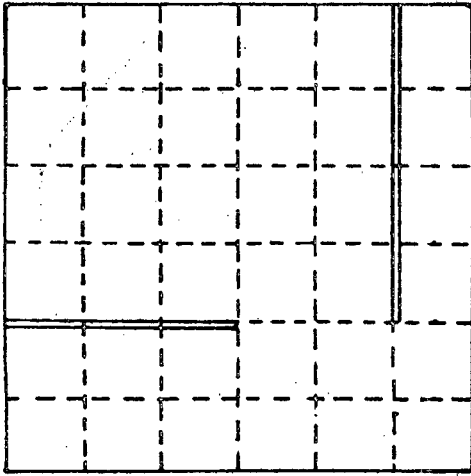
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Problem 11



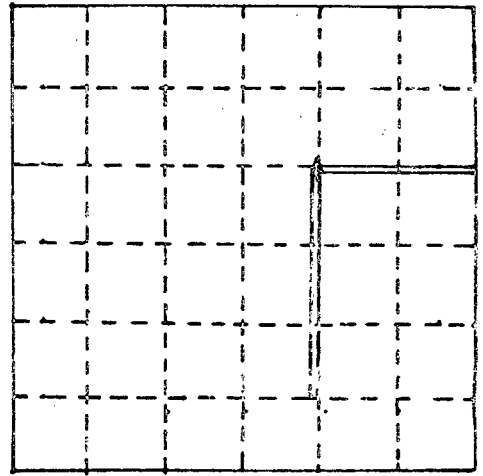
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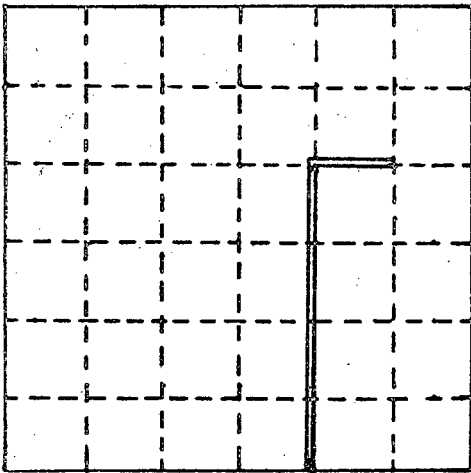
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Problem A



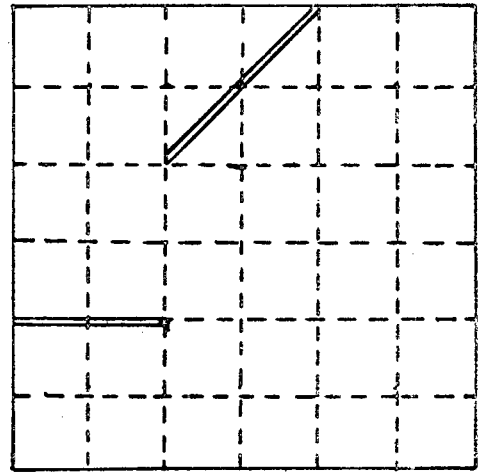
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Problem B



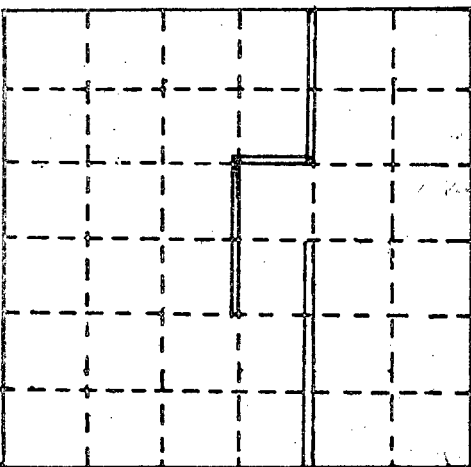
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Problem C



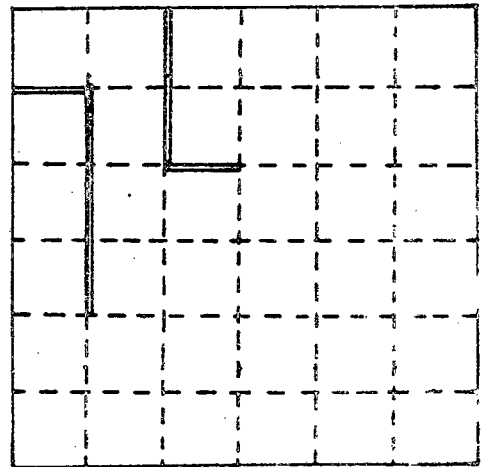
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Problem D



S

Problem E



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Problem F

Table A
Defecation scores on the open field test

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	5,00	2,60	2,80	2,60	
2	3,00	3,20	3,20	1,30	
3	2,40	1,80	2,10	2,70	
4	5,00	3,40	4,00	2,50	
5	3,10	3,60	3,20	3,10	
6	3,80	2,30	2,80	3,50	
Control					
Trial	C1	C2	C3	C4	
1	6,30	4,40	8,90	6,10	
2	7,20	5,20	7,80	5,90	
3	4,80	3,80	7,90	4,70	
4	3,10	6,10	8,50	6,90	
5	5,10	5,50	6,80	6,30	
6	3,90	3,80	7,90	7,00	

Table 8

Grooming scores on the open field test

140

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	1,00	1,20	1,30	1,40	
2	1,60	1,90	2,00	1,50	
3	1,60	1,50	1,00	1,10	
4	2,50	1,00	1,70	1,70	
5	2,80	1,00	3,00	0,80	
6	2,80	1,20	2,30	1,00	
Control					
Trial	C1	C2	C3	C4	
1	4,10	2,70	4,30	2,30	
2	2,70	2,90	5,90	4,00	
3	3,50	3,00	5,00	1,80	
4	3,70	3,50	3,90	2,50	
5	2,00	1,80	3,80	1,50	
6	3,10	3,20	4,30	2,80	

Table C

Rearing scores on the open field test

141

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	9,70	10,50	6,20	8,30	
2	7,80	9,80	5,20	2,50	
3	4,20	10,60	4,90	1,20	
4	6,30	3,90	3,10	10,70	
5	6,10	6,50	6,80	6,00	
6	9,90	4,00	8,90	3,90	
Control					
Trial	C1	C2	C3	C4	
1	7,50	5,90	4,20	6,90	
2	8,30	4,80	3,80	5,10	
3	4,70	5,50	4,80	4,90	
4	3,90	5,70	4,70	3,80	
5	8,10	5,00	3,90	3,00	
6	6,30	6,10	3,70	4,20	

Table D

Ambulation scores on the open field test

142

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	79,10	60,70	38,20	24,70	
2	56,90	57,20	35,00	14,70	
3	27,10	47,90	35,90	7,50	
4	38,40	20,80	40,10	34,80	
5	21,30	17,50	27,30	20,50	
6	28,60	13,60	30,20	15,30	
Control					
Trial	C1	C2	C3	C4	
1	30,30	23,50	10,30	15,70	
2	22,40	21,90	11,50	19,20	
3	32,30	17,80	9,90	10,30	
4	24,10	22,80	13,00	13,90	
5	26,20	20,00	11,20	17,10	
6	29,40	20,70	8,90	18,30	

Table E

Latency scores on the open field test

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	11,80	9,00	6,00	8,80	
2	6,30	3,50	8,00	9,00	
3	1,80	1,70	7,00	3,80	
4	1,20	2,20	8,00	4,30	
5	1,00	1,60	3,00	3,20	
6	1,00	2,00	2,50	5,70	
Control					
Trials	C1	C2	C3	C4	
1	5,10	6,10	8,90	6,50	
2	4,90	4,90	8,10	7,20	
3	6,00	5,60	7,80	6,90	
4	7,10	5,70	8,60	8,00	
5	3,20	5,10	8,30	6,70	
6	4,50	6,20	7,90	5,90	

Table F

Time (seconds) scores on the Hebb-Williams test

144

Trials		Groups			
Experimental					
Trial	E1	E2	E3	E4	
1	6,65	7,15	7,29	7,52	
2	9,98	10,42	10,78	9,46	
3	7,02	8,43	8,52	6,98	
4	9,49	10,16	9,22	12,46	
5	10,37	15,52	10,44	22,00	
6	11,39	10,89	13,00	13,19	
7	7,17	7,99	8,72	9,25	
8	11,45	13,24	13,57	11,37	
9	13,22	11,31	11,55	12,38	
10	11,40	11,20	11,00	12,00	
11	10,97	11,10	10,50	10,79	
12	14,11	19,35	23,52	21,31	
Control					
Trial	C1	C2	C3	C4	
1	8,25	7,27	6,97	8,98	
2	10,10	9,38	9,98	11,87	
3	7,36	7,79	7,28	7,66	
4	14,92	13,29	13,76	12,21	
5	23,75	22,77	23,15	23,31	
6	12,79	13,21	13,22	14,74	
7	9,00	10,12	9,78	10,00	
8	11,27	10,58	12,12	11,22	
9	13,54	13,21	12,99	13,45	
10	13,39	11,99	13,32	13,71	
11	10,19	11,23	11,30	12,74	
12	20,42	21,28	22,73	25,72	

Table G

Squares scores on the Hebb-Williams test

Trials		Groups			
		Experimental			
Trial	E1	E2	E3	E4	
1	7,90	7,83	8,99	7,23	
2	12,15	13,25	14,22	10,38	
3	9,62	11,11	10,66	10,15	
4	15,71	14,99	13,89	13,79	
5	13,03	19,29	13,97	20,88	
6	18,50	17,89	20,01	22,20	
7	13,60	14,00	14,98	12,00	
8	19,89	21,25	22,33	20,23	
9	23,35	20,27	17,32	16,11	
10	19,73	19,01	19,02	22,41	
11	15,47	16,24	14,14	13,31	
12	21,26	20,97	24,00	22,23	
		Control			
Trial	C1	C2	C3	C4	
1	9,40	8,74	7,10	9,21	
2	13,01	12,71	10,45	11,33	
3	11,29	11,38	11,00	13,31	
4	13,78	11,00	14,29	13,55	
5	21,97	22,33	22,31	22,98	
6	20,75	24,11	23,10	23,38	
7	10,29	13,57	12,33	11,98	
8	21,30	18,79	20,29	18,29	
9	18,21	19,12	16,76	11,87	
10	24,22	20,25	23,56	23,23	
11	12,13	15,78	14,21	15,43	
12	21,39	22,22	23,97	24,93	

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